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Effect of spatial and non-spatial changes on perceived self-location

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Effect of spatial and non-spatial changes on perceived self-location

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The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

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NOMENCLATURE

VR	Virtual Reality
VE	Virtual Environment
SAE	Sensorimotor Alignment Effect
JRD(s)	Judgement(s) of Relative Direction

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ABSTRACT

Place cell activity is measured through single-cell recording in animals, though place-responsive cells and related properties have been identified in the human hippocampus. Human behavioral studies would strengthen these findings, especially given the challenge of conducting neuroscientific research on human place-responsive cells. The current study was based on the finding (Lenck-Santini et al., 2005) that rodent place cells partially remap after spatial environmental changes (rotating objects relative to enclosure) but are unaffected by non-spatial changes (object substitution). In two completed studies, human perceived self-location was evaluated in response to spatial and non-spatial changes in a virtual environment (VE). Participants studied object locations in a learning VE with three orienting cues: two landmarks and a featural cue (blue stripe on the wall of the surrounding circular room). Participants then performed judgments of relative direction (JRD) in which they imagined various perspectives using the learned object locations. The JRD task was performed while standing in one of four test VEs which varied in spatial and non-spatial changes relative to the learning VE. Perceived self-location was inferred from the presence/absence of a sensorimotor alignment effect (SAE), indicated by facilitation for imagined perspectives aligned with the body at retrieval. It was expected that the SAE would be present in non-spatial change VEs and absent in spatial change VEs. As predicted, results indicated that non-spatial changes did not disrupt perceived self-location (SAE present). Spatial changes did disrupt perceived self-location (SAE absent), but this effect appeared to depend on participant view at test.

CHAPTER 1. INTRODUCTION

The majority of species effectively navigate across vast environments by relying on strategies that take advantage of available sources of information. External information, such as visual cues (e.g., proximal and distal landmarks) and the geometric structure of the environment is one source. Another source originates from self-movement cues, which include optic flow (visually experienced movement through the environment), proprioception (sense of body position and effort in movements), and vestibular cues (Wolbers & Hegarty, 2010). For example, the desert ant (*Cataglyphis*) can travel several meters in a curvilinear, outward path and then return in a linear, homeward path. This feat utilizes by path integration, a process which integrates body-based self-motion cues over time and polarized light from the sun to sense direction (Wehner, 2003). These multiple sensory signals input to various cellular networks and combine to form an internal spatial representation or cognitive map of the environment.

An animal's self-localization, or understanding of its position in space relative to the surrounding environment, was based on Tolman's (1948) theory that mammals use spatial information as if it was stored in a map-like fashion. This theory, which was subsumed to be an integration of spatial knowledge and personal experiences, was elucidated in rodent behavior. A rat was trained to follow a path in a maze to a specified location where the rat was rewarded with food. After four days, the maze was altered. The original path was blocked and 12 arms radiated from the central arena. Prevented from using the original path, the rat explored the environment until it selected a new arm and traversed the entire length. Nineteen of the 53 rats (36%) chose the arm closest in distance to the original path (i.e., the selected arm had a location about four inches from

the original location). This result suggests that the rats acquired knowledge of the direction of the original location, and selected a new path with a location spatially close to the original location (Tolman, Ritchie, & Kalish, 1946). The rodent brain appeared to form a representation of the rat's current position while simultaneously integrating the rat's previous experience with the original location into a "shortcut" the rat had never experienced (i.e., the entire length of the new radial arm). This combination of spatial information and personal experiences encouraged Tolman (1948) to refer to a theory of how we represent our surrounding environment as a metaphorical cognitive map. Humans are also quite adept at representing shortcuts in familiar environments. A conceptually similar paradigm is the triangle completion task, which requires participants to traverse two path legs then indicate the origin, usually by walking or pointing. Performance is typically accurate, with an average heading error of about 10˚ when participants physically walk and turn to complete the task (Klatzky, Loomis, Beall, Chance, & Golledge, 1998).

Animal Research on Place Cells

The theory of a cognitive map was further specified by work which suggested that the hippocampus serves as a map-like representation of space (O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978). The mammalian hippocampus consists of two "C-shaped" parts, the *cornu ammonis* (CA) fields, and it is currently suggested that around 11-25% of neurons in the human hippocampus and parahippocampal regions respond purely to spatial locations (Ekstrom et al., 2003; Miller et al., 2013). To characterize the role of the hippocampus as a representation of space, O'Keefe, and Dostrovsky (1971) used electrophysiology, a process which measures electrical activity associated with activity in the body, to access single pyramidal cells in the dorsal hippocampus (CA1 and

4). By inserting microelectrodes into a rat brain, they were able to record action potentials extracellularly. Wires from a preamplifier were attached to recording equipment and displayed firing in real-time, while postmortem histology confirmed the location of recording sites. Out of 76 recorded units, eight cells were of interest due to their preferential firing in a specific location relative to non-existent firing, or silence, across other locations. Novel tactile (e.g., placing a hand on the rodent), visual (e.g., rotating the platform, dimming light sources), and olfactory stimuli were either introduced or removed in an attempt to alter cell firing, but these unique variations in sensory information did not produce a differential firing response in those cells. Thus, these cells appeared to not rely preferentially on any single sensory input but instead weighted them equally as evidenced by the inability to disrupt firing through single cue alteration. Only the manipulation of several items in the environment, such as varying the size and shape of the animal's environment, elicited altered firing responses of recorded cells. From these results, O'Keefe and Dostrovsky (1971) proposed that the hippocampus functions as a spatial map.

The cells of interest in O'Keefe and Dostrovsky's (1971) experiment that fire preferentially based off of an animal's occupied location in an environment were first referred to as "spatial cells" (see Figure 1). This name would later be refined to the current concept of "place cells." The discovery of place cells in the hippocampus was regarded as a prime example for the role of the hippocampus in the formation of a cognitive map and the beginning of several investigations into elucidating single cell responses from the hippocampus and surrounding regions (Eichenbaum, 2017; O'Keefe & Nadel, 1978). Additional evidence for the hippocampus serving as a neural

representation of space came from discoveries of a class of cells that respond to the direction that an animal is facing at a given time, aptly named “head direction cells” (Muller, Ranck Jr., & Taube, 1996; Taube et al., 1990a, 1990b).

More recently “grid cells” have also been found in regions within the hippocampal system (e.g., the medial entorhinal cortex (MEC) and in the pre- and parasubiculum) (Boccara et al., 2010; Moser, Rowland, & Moser, 2015; Hartley, Lever, Burgess, & O’Keefe, 2014). Grid cells fire in a hexagonal pattern when an animal navigates a given space and are presumed to support place cell formation through additive firing (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Solstad, Moser, & Einevoll, 2006). The importance of refining the role of the hippocampus was recognized in 2014 when the Nobel Prize in Physiology or Medicine was awarded to John O’Keefe and May-Britt and Edvard Moser for their discoveries of cells that constitute a “positioning system” in the brain. These findings have led to the view that the hippocampus and surrounding structures represent an internal system that supports spatial navigation.

For this paper, the focus will be primarily on experiments that have investigated properties of place cells. Place cells denote a location in the environment by combining several sensory inputs (O’Keefe, 1979), and though place cells are typically recorded from the hippocampus, these cells have also been found in additional regions, such as the dentate gyrus and MEC (Grieves & Jeffrey, 2017; O’Keefe, 1979; Park, Dvorak, & Fenton, 2011). One property of place cells is stability over time. For example, Thompson and Best (1990) recorded a single place cell that fired in the same location during 14 independent sessions over 153 days (about five months). However, if the environment

changed (e.g., altered geometric shape) place cells can change the location of their firing, or cease entirely, and represent the space uniquely (Anderson & Jeffrey, 2003; O'Keefe & Conway, 1978; Wills, Lever, Cacucci, Burgess, & O'Keefe, 2005) (see Figure 2). This process of differential firing based on altered environments is referred to as "remapping" (Muller & Kubie, 1987). This phenomenon of remapping appears to be unpredictable, since researchers cannot reliably predict where (or if) a particular place cell will fire in a novel environment.

Remapping in place cells is unique, and this is especially evident when compared to firing properties from head direction cells. For example, if the geometric configuration of space is altered (e.g., change from a circular environment to a rectangular environment), head direction cells will not cease firing or change location (Taube et al., 1990b). Instead, head-direction cells have been shown to rotate along with the environment to preserve the cell's preferred firing direction. For example, the rotation of a cue card produced almost near-equal rotation in the preferred firing direction of head-direction cells (Taube et al., 1990b). Conversely, two place cells that represent adjacent locations in one enclosure may not represent adjacent locations in a different enclosure. In fact, place cells might not even respond at all. However, this change in place cell firing between distinct environments can revert to the original firing pattern if the animal is re-introduced to the original environment (Muller & Kubie, 1987; O'Keefe & Conway, 1978). In other words, if the animal recognizes a space, then place cell firing will demonstrate the original firing patterns. These observations suggest that an animal can either recognize its occupied space, if place field firing is consistent across time, or regard the space as novel or distinct if place field firing changes. Therefore, place cells

are presumed to be a mechanism within the hippocampus that can distinguish locations both within and between environments.

The majority of research concerned with understanding the neuronal representations of space have been based on experiments with rats and mice; however, experiments investigating place-related activity in non-human primates have yielded results consistent with rodent studies. Hori et al. (2005) recorded cells within the hippocampal formation in two adult monkeys (*Macaca fuscata*) as they performed goal-oriented navigation tasks projected on a screen. Three environments were displayed, with different arrangements of distal landmarks to distinguish the arenas. The recordings indicated place-related activity within the hippocampus formation across the virtual arenas that were consistent with remapping observed in rodent place cell activity across unique environments. These findings suggest that non-human primates have neuronal representations of space that respond similarly as the place cells recorded in rodents across spatially distinct environments. It appears that knowledge from place cell recordings in rodents can inform predictions for larger, more complex mammals, such as non-human primates.

Furthermore, virtual reality (VR) has been immensely popular as a tool to investigate and understand real-world spatial cognition. Several studies have shown that the use of VR compliments spatial phenomena typically studied in the real world, such as the sensorimotor alignment effect (Williams, Narasimham, Westerman, Rieser, & Bodenheimer, 2007) and spatial updating (Ruddle & Lessels, 2006).

Human Research on Place Cells

Although most prior research on place cells used single-cell recordings in mammals, research with humans also corroborates these findings. The current view of the

role of the hippocampus in humans is thought to be involved in more general memory, including spatial functions essential to navigation. For example, atrophy in the hippocampus is often associated with neurodegenerative diseases, such as Alzheimer's disease (Fox et al., 1996). Patients with a damaged hippocampus often exhibit difficulty in forming new, long-lasting memories of personally experienced events as well as deficits in spatial orientation and navigation (Scoville & Milner, 1957; Spiers, Maguire, & Burgess, 2001; Vargha-Khadem et al., 1997). Based on these observations, the human hippocampus appears to support navigational systems and warrants further investigation for the presence and function of neuronal representations of space that complement the neuronal mechanisms extensively studied in other mammals.

Methods for understanding spatial cognition in the human brain have included functional neuroimaging, such as functional magnetic resonance imaging (fMRI) which allows for imaging of the entire brain for the study of structural relations. For example, participants given active spatial tasks demonstrate activation within the hippocampal formation (Hartley et al., 2014). Other functional neuroimaging methods, such as positron emission tomography (PET) which detects areas of high blood flow in the brain, have also established correlations between activation in the right hippocampus and goal-oriented navigation (Maguire et al., 1998).

Other studies with humans have used more direct measures, such as intracranial electrophysiology, a process where microelectrodes are implanted (usually into an epileptic patient's brain to identify seizure origins). Once these microelectrodes are implanted, it is possible to record the activity of individual neurons while participants perform various tasks. Ekstrom et al. (2003) directly recorded 317 neurons in seven

epileptic patients while they performed a navigational “taxi-driver” game in a virtual town. Targeted brain regions included the hippocampus, parahippocampal region, amygdala, and areas in the frontal lobes (e.g., anterior cingulate, orbital frontal cortex, and supplementary motor cortex). To approximate cellular function, spike rates were compared as a function of the participant’s location in the virtual town (place), the object viewed (view), and target (goal).

Several cells responded to place and view, but to qualify as solely place-responsive, it was imperative that the recorded cells did not respond to view of an object and location or goal and location. About 11% of the total recorded cells fit the criteria for place-selectivity (31 out of 279), and these cells were found at a significant frequency in the hippocampus. Within the hippocampus, around 24% of recorded cells were identified as place-responsive cells. These results suggest that the human hippocampus has place-responsive cells that can form a flexible map-like representation of space. Overall, these studies have established an emerging model of the physiological basis of human navigation, and a next step is to test established predictions about neural responses in animals in human behavior. If similar properties are observed between human behavior and animal studies, then these results will provide converging evidence for characterizing the mechanisms of human navigation.

One such convergence came from the study of attractor dynamics in the hippocampus and its role in the formation of distinct spatial contexts. Place cell firing was measured in rodents exposed to novel square and circular environments that differed in color and texture (Wills et al., 2005). It was hypothesized that exposure to the square or circular environment would establish attractor representations and place cells would

fire distinctly in each environment. The results showed that place cells did fire distinctly and could abruptly switch representations when the rodent was placed in either environment. To investigate whether intermediate room shapes (e.g., an octagon) would exhibit the distinct representations of either the square or circular environment, place cell firing in four intermediate room shapes were also recorded. Results showed that place cells did exhibit a switch from the squarelike to the circlelike pattern across the series of intermediate room shapes. These results suggest that attractor dynamics can influence representations of intermediate or ambiguous spaces, which could aid in reducing interference by creating orthogonal representations of spatially-relevant contexts.

This observable difference in rodent spatial representation fueled investigations into whether human memory retrieval is also driven by similar mechanisms (e.g., attractor dynamics). Participants performed a behavioral task while lying in an fMRI scanner where objects were learned relative to specific locations within two distinct VEs (Steemers et al., 2016). During testing, participants were asked to place each object in its learned location in the two distinct VEs as well as four morphed VEs which resembled intermediate versions of the two distinct VEs. The results showed that there was an abrupt shift in object location representation across the morphed VEs, which suggests that the hippocampus has a remapping-like response to linear changes in spatial contexts. These experiments demonstrated that properties of rodent place cells (e.g., attractor dynamics) could be observed in human behavior.

Though research on human spatial cognition has utilized advanced technology (e.g., fMRI), these methods can be costly. Human behavioral studies would strengthen these findings, especially given the challenge of conducting neuroscientific research on

human place-responsive cells since those studies are rare and typically involve immobile patients. One example of successfully predicting human behavior from animal neuroscience came from grid cell properties initially obtained from a study with rodents (Barry, Hayman, Burgess, & Jeffery, 2007). When an environment expands or contracts, grid cell firing in rodents will parametrically expand or contract in accordance with the now "deformed" environment (i.e., if space expands after it has been adequately explored, grid cells will expand their firing along the axis of the room that has expanded and vice versa with contracted spaces).

Based on these grid cell properties, Chen, He, Kelly, Fiete, and McNamara (2015) predicted that humans would exhibit similar biases. After experiencing the original "primed" room in VR, participants walked an outbound path in a deformed room that was stretched or compressed along one axis. Participants executed the homeward path to the origin in the absence of visual cues (i.e., the room was removed from view), and researchers predicted response biases that would either undershoot or overshoot the origin depending on whether the room had been stretched or compressed. The results demonstrated that path responses did show a bias in accordance with the predictions derived from grid cell properties. For example, if the deformed space was smaller than the original familiar space and the participant had restricted vision while walking to the origin, the participant tended to overshoot the goal location since the original grid cell pattern had presumably been reinstated once the deformed space was removed. The results of Chen et al. (2015) demonstrate that human behavioral predictions can be made from animal literature on the neural mechanisms of spatial navigation.

Current Study

If human perceived self-location is informed by place-responsive cells that have similar properties to place cells found in rodents, then modifying a familiar environment in a way that elicits a change in place cell firing in rodents should also cause humans to perceive the modified environment as distinct. The current study used environmental modifications (e.g., spatial changes) shown to cause changes in place cell firing in rats and evaluated whether those environmental modifications affected perceived self-location. Currently, there is a dearth of converging evidence from the animal neuroscience literature and human navigation behavior. The current study aimed to bridge this knowledge gap and add to the existing literature on human spatial cognition.

Studying human perceived self-location requires an operational definition. The simplest way to measure human perceived self-location is to ask, "Where do you think you are?" However, such requests are likely to create demand characteristics. Therefore, this study used an implicit measure of perceived self-location based on the sensorimotor alignment effect (SAE), an established effect that reflects the perceived location of the respondent (Kelly, Avraamides, & Loomis, 2007). The SAE is best illustrated by an example. Please pay attention to the location of two objects around you, such as the door to your office and your office phone. Make sure that you are not currently facing the door to your office. Now, perform the two following imagined perspective-taking trials. First, close your eyes and point to the location of your door. Next, close your eyes, *imagine* rotating your body until you are facing the door and then point to your phone as if you occupy that new imagined perspective. The first trial should have been easier than the second trial, and this is an example of the SAE. For our purposes in the current study, the SAE is applied regarding an advantageous effect of imagined perspective aligned with

the physical body (i.e., an advantage of making spatial judgments when the body is aligned with the imagined perspective during retrieval). Spatial judgments tend to increase with difficulty as the imagined perspective deviates absolutely from the body, as you may have experienced in the example illustrated above. These deviations in perspectives are referred to as imagined perspectives misaligned with the body or body misaligned perspectives. An example of a spatial judgment typically used in the SAE is judgments of relative direction (JRDs). This task involves asking participants to imagine a specific location and orientation and then point to another location/object from that perspective (e.g., "Imagine standing at Physics hall, facing the Memorial Union, point to Parks library").

The current study inferred perceived self-location through the use of the SAE. It was predicted that similar environments should facilitate the presence of the SAE, and different environments should eliminate the SAE. This prediction was supported by Kelly et al. (2007) who asked participants to learn several objects within one VE and then investigated the SAE when object location retrieval occurred while the participant stood either in the learning environment (the objects were removed before testing) or a novel environment. Participants were asked to make judgments about remembered object locations by imagining facing one object and then indicating with a joystick the direction of the second object from that imagined perspective. The results showed a presence of the SAE in the learning room, with an advantage for perspectives aligned with the participant's actual facing direction at the time of retrieval, but no SAE in the novel room (i.e., no advantage for aligned versus misaligned perspectives). These results suggested that presence or absence of the SAE during memory retrieval indicates whether the

participant believes he/she is in a location that resembles the learning environment (the environment in which the remembered objects were learned) or a novel environment.

A recent study by Riecke and McNamara (2017) found that the SAE can be instated in participants who experience a real, remote room that differed in both scale and appearance from the real learning room. Participants first learned object locations in a rectangular room, were disoriented and moved to a remote, sparse (i.e., contained none of the learned objects) test room that resembled the learning room. The results showed that participant JRDs were more accurate for imagined perspectives that were aligned with the participant's physical facing direction during testing than imagined perspectives that were misaligned with physical facing direction. In a follow-up experiment, participants studied the same objects in the previous learning room, were disoriented, and moved to a remote test room that was still rectangular but larger in scale and cluttered with random objects that differed from the learned objects. The results showed that participant JRDs were still more accurate for imagined perspectives that were aligned with participant physical facing direction but to a lesser extent. These results suggest that changing aspects of a test environment (e.g., room scale, adding novel objects) can reduce the magnitude of the SAE, but preserving other aspects (e.g., room shape) can facilitate SAE presence. Therefore, the SAE appears to depend on the similarity between the learning and test environments, with more similar environments yielding a larger SAE. Based off these results, the SAE will be used as a proxy in the current study for the perception of self-location, with the prediction that similar environments will yield the SAE and distinct environments will not yield the SAE.

In sum, if the SAE is present in a testing environment that resembles the learning environment, the presence implies that the participant believes that he or she is in an environment that is comparable to the learning environment. Hence, the participant registered these two environments similarly. If the SAE is absent, it suggests that the participant believes that he or she is in a different space (i.e., an environment that is distinct from the learning environment). An absence of the SAE would imply that the participant registered the two environments as distinct or unique.

The current study explored the effect of environmental manipulations on perceived self-location in VR. The selected environmental manipulations are based on rodent research evaluating the effects of similar manipulations on place cell activity (Lenck-Santini, Rivard, Muller, & Poucet, 2005). If human perception of self-location is influenced by neurons similar to the rodent place cell system, then manipulations that disrupt rodent place cells might also affect human perception of self-location, and the contribution of this work will further characterize the neural mechanisms underlying human navigation through means of behavioral predictions informed from animal neuroscience.

One of the properties of place cells is the ability to fire differentially across unique environments, referred to as remapping. The process of remapping can be best characterized by recording from place cells during repeated visits to one environment, and recording the same place cells in a novel environment and correlating the firing fields. Place cell firing should be highly correlated across repeated visits to the same environment, but uncorrelated across two unique environments. Lenck-Santini et al. (2005) hypothesized that the hippocampus might be more sensitive to detecting

differences in spatial arrangements than to object substitution. When introduced to a novel environment, rats will freely explore the space until, over time, exploratory behaviors are reduced. It is then presumed that the animal has habituated to the environment (i.e., encoded and stored critical properties of the space). The existence of a stored representation after initial exploration is evidenced by potential reexploration, which occurs after spatial changes (e.g., shift object locations) and non-spatial changes (e.g., object substitution) to the habituated environment (Poucet, Chapus, Durup, & Thinus-Blanc, 1986; Thinus-Blanc et al., 1987). If the hippocampus is damaged, reexploration of the environment is reduced or eliminated for rats after spatial changes in a learned environment, but reexploration occurs after non-spatial changes (Save, Poucet, Foreman, & Buhot, 1992). Therefore, Lenck-Santini et al. (2005) predicted that a spatial change would disrupt locational place cell firing in the hippocampus, while a non-spatial change would not affect locational place cell firing.

Lenck-Santini et al. (2005) recorded place cells in the CA1 of the hippocampus in rats across three environments. Rats were first familiarized in a cylindrical arena that contained two distinct objects and a featural cue card attached to one wall. After exposure to the first environment, rats were removed and placed into another environment where both objects rotated 90˚, disrupting the original spatial relationship between the objects and the card. Rats were also exposed to a third environment where one of the original, familiar objects was replaced with a novel object, but preserved the spatial relationship between the objects and the featural cue card (see Figure 3).

After excluding cells that were either lost too early during the experiment or fired too scarcely, the resulting cells were analyzed across sessions. Object substitution had

little to no discernable effect on place cell activity regardless of the firing field's proximity to the substituted objects. For object rotation, some place cells were unaffected while other place cells showed partial remapping (see Figure 4). Unaffected place cells were mostly located near the border of the environment or far away from the rotated objects. Place cells that were affected by object rotation were typically close to the objects or located in between them. The results of the experiment suggest that changes in place cell firing occurred near and between the two rotated objects, and little to no changes in place cell firing occurred during object substitution regardless of proximity to the substituted objects. Lenck-Santini et al. (2005) proposed that the featural cue card provided a stable reference frame that kept the far firing field intact compared to the near-firing fields that were modified by the object rotation. These results suggest that spatial changes (object rotation) cause partial remapping in place cells while non-spatial changes (object substitution) leave place cells unaffected.

CHAPTER 2. EXPERIMENT 1

Motivated by the results of Lenck-Santini et al. (2005) that object rotation, but not object substitution, caused partial remapping, the current study investigated the effects of object rotation and substitution on human perception of self-location. Human perceived self-location is presumed to be informed by a combination of several external and internal cues, such as place-responsive cells (Ekstrom et al., 2003). Therefore, investigations connecting properties from animal neuroscience on place cell activity to behavioral measures of perceived self-location warrant further investigation.

Participants learned the locations of small objects placed on the floor of a VE, referred to as the learning environment. The learning environment (see Figure 5) consisted of a circular room with three distinct cues: a featural cue (blue stripe on one wall) and two landmarks (plant and cone). In this way, the layout was conceptually similar to the initial environment used by Lenck-Santini et al. (2005). After learning, participants were disoriented and randomly placed into one of four test VEs (see Figure 6). The four test VEs included an unchanged condition (no change condition) that was visually identical to the learning VE (see Figure 6, top left panel), an object rotation condition (see Figure 6, top right panel), a stripe rotation condition (see Figure 6, lower left panel), and an object substitution condition (see Figure 6, lower right panel).

The hypotheses for this study follow the results of Lenck-Santini et al. (2005). A participant tested in the no change condition should demonstrate facilitated JRD performance with the presence of the SAE (i.e., response errors should be the lowest when the participant's body is aligned with the imagined perspective). Similar results would be expected for participants tested in the object substitution condition since the

spatial arrangement was preserved from the learning VE. Participants tested in the object rotation condition should not exhibit the SAE since the spatial arrangement from the learning VE was disrupted, leading participants to perceive the surrounding VE as distinct. The stripe rotation condition was not initially included in the study by Lenck-Santini et al. (2005), and a prediction for this condition follows the prediction for the object rotation condition since the spatial arrangement was also disrupted from the learning VE.

Hypothesis 1A: If the spatial arrangement is not disrupted from the learning VE (e.g., no change and object substitution conditions), the SAE will be present, indicating participants regard the test VE as similar to the learning VE.

Hypothesis 1B: If the spatial arrangement is disrupted from the learning VE (e.g., object and stripe rotation conditions), the SAE will be absent, indicating participants regard the test VE as distinct from the learning VE.

Method

Participants

Seventy-one undergraduate students from Iowa State University (F = 42) participated in exchange for course credit. The first 64 participants were randomly assigned to one of the four test conditions. Data from seven participants (F = 4) were removed after outlier analysis (see Results). After outlier removal, additional participants were assigned to fill out the conditions that lost participant data. The final sample was 64 (F = 38), and the size of each condition was as follows: no change condition (n = 16, F = 10), object rotation condition (n = 16, F = 10), stripe rotation condition (n = 17, F = 9), or object substitution condition (n = 15, F = 9). Gender was approximately balanced across

conditions. This project was approved by the Iowa State University's Institutional Review Board (see Appendix).

Stimuli and Design

The VEs were displayed on an HTC Vive HMD. Graphics displayed in the Vive were generated on a Windows 10 computer with an Intel 6700K processor and Nvidia GeForce GTX 1070 graphics card. Vizard (Santa Barbara, CA) software displayed stereoscopic images at 1080 x 1200 resolution with 100˚ horizontal x 110˚ vertical. Images refreshed at a rate of 90 Hz and reproduced head movement and orientation of participants as they navigated the VE.

Each VE had the same dimensions (11.4m diameter x 7.5m height) and texture on the floor, wall, and ceiling. The five VEs included a learning VE, a no change condition (see Figure 7, top left), an object rotation condition (see Figure 7, top right), a stripe rotation condition (see Figure 7, lower left), and an object substitution condition (see Figure 7, lower right). In the learning VE, the two landmarks (plant and cone) were placed 2.5m from the center of the room, with a total of 5m of distance between them. The no change condition was the same as the learning VE where participants learned the small object locations. In the object rotation condition, both the plant and the cone rotated 90˚, with the cone in front of the blue stripe on the wall. In the stripe rotation condition, the blue stripe was rotated 90˚ to be beside the cone, and the two landmarks remained in the original position. Lastly, in the object substitution condition, the spatial arrangement was preserved from the learning VE, but the cone was replaced with a fire hydrant.

Participants learned locations of seven small objects (e.g., tape, stapler, penguin, ball, CD, book, and mug) organized into a pattern on the floor (see Figure 8) in the

learning VE. Objects were presented one at a time during learning to reduce any initial reference frame formation.

There were 48 different JRD trials with 15 trials for the 90˚ imagined perspective, 15 trials for the 270˚ imagined perspective, and three trials each for other imagined perspectives (e.g., 0˚, 45˚, 135˚, 180˚, 225˚, & 315˚). Although the 90˚ and 270˚ imagined perspectives were of primary interest, the other perspectives were included to make the task less predictable and to evaluate performance at other imagined perspectives if needed. The set of 48 trials was performed twice in two separate blocks, once while physically facing 90˚ and once while facing 270˚. Order of physical facing direction was counterbalanced, and trial order within blocks was randomized.

The dependent variables were absolute pointing error and response latency. To indicate the direction of the object during JRD trials, participants deflected a joystick mounted on a wooden box (12in x 12in x 36in).

Procedure

After signing the informed consent, the participant was given verbal instructions on the JRD task. To practice, the participant was asked to name three buildings on campus he or she was familiar. The experimenter then used the selected buildings for a practice JRD task, and the participant was instructed to respond using the joystick. Once the participant gave verbal confirmation of understanding the JRD task, the participant donned the HMD. Beginning in the center of the VE, the experimenter physically guided the participant to the landmarks and featural cue and paused so that the participant could view the entire VE from that location before moving to the next cue. The participant was then led back to the center of the room to begin learning.

During the first phase of learning, each participant physically walked to each of the small objects, with landmarks and featural cue present, which ensured that the participant knew the name of the object and its location. Once the participant physically walked to all of the small objects, the second learning phase began. The experimenter hit a key on the keyboard which presented the name of a randomly selected small object solely to the experimenter. The experimenter asked the participant to walk to his or her perceived location of the small object. Once the participant verbally confirmed that he or she was satisfied with the perceived location of the small object, the experimenter revealed the small object's location. The participant adjusted position if needed. Learning was repeated at least three times for all of the small objects. The experimenter subjectively judged whether the participant had sufficiently learned each small object's location, and administered another round of learning if needed.

Once learning was determined sufficient by the experimenter, he or she hit a key on the keyboard and removed all visual input in the HMD. The experimenter disoriented the participant for 20 seconds by spinning the participant in a circle, alternating clockwise and counter-clockwise directions. The experimenter also instructed the participant to count backward from a randomly generated number (e.g., 254) by increments of seven (e.g., "254, 247, 240, 233…"). During disorientation, the participant remained in the center of the lab space.

After disorientation, the experimenter hit a button on the Vive controller which displayed one of the four randomly assigned test VEs. The experimenter physically guided the participant to the landmarks and featural cue within the test VE. If a landmark was now near the featural cue (e.g., the cone next to the blue stripe), the participant was

led to that location only once. After exploring the VE, the participant walked to the center of the VE. The experimenter pushed a button on the Vive controller, and a block of text appeared for either the 90˚ or 270˚ physical facing direction. The participant faced the text, and the experimenter placed the joystick stand in front of the participant. The participant then completed 48 JRD trials.

Once the participant completed the JRD trials, the text disappeared, and the experimenter instructed the participant to turn 180˚ to face either the 90˚ or 270˚ physical facing direction (the next physical facing direction was dependent on which facing direction had appeared first). The experimenter pressed another button on the Vive controller, and a new block of text appeared. The experimenter moved the joystick stand, and the participant began the next 48 JRD trials. Once the JRD trials were completed, the participant removed the HMD, was debriefed, and given course credit.

Analyses

The two dependent variables were absolute pointing error and response latency. Absolute pointing error was calculated by subtracting the participant's pointing response from the correct response and taking the absolute value. If pointing error was greater than 180˚ the value was subtracted from 360˚, and if pointing error was less than 180˚ no further calculations were performed.

SAE presence was examined for JRD trials that were considered "body aligned" and "body misaligned." Body aligned trials were those in which the physical facing direction (e.g., 90˚) matched the imagined perspective (e.g., 90˚). Body misaligned trials were those in which the physical facing direction (e.g., 90˚) was 180 ˚ misaligned with the imagined perspective (e.g., 270˚). For outlier detection, a paired sample t-test compared individual participant trial performance to chance (90˚) on each trial. If

participant performance was not statistically different from chance performance, the data were excluded from further analysis.

Effect sizes, Cohen's $d_{average}$ (Cohen's d_{av}) and Hedge's $g_{average}$ (Hedge's g_{av}), were reported for paired-samples t-tests. Hedge's g_{av} was reported to correct for an overestimation of effect sizes and has been suggested for small sample sizes (< 20) (Lakens, 2013).

Results

Data from seven participants were removed after outlier analysis. There were four (F = 1) from the object rotation, one (F = 1) from the stripe rotation, one (F = 1) from the no change, and one (F = 1) from the object substitution conditions. There was also no evidence of a speed accuracy tradeoff. The within-participant correlation between pointing error and response latency was significantly positive (M = .21, SE = .07), $t(63)$ = 2.71, p = .009. Pointing error was more responsive to the independent variables, though response latency generally supported the same conclusions, and so the focus is on pointing error.

As predicted, the SAE occurred in the no change and object substitution conditions. Contrary to predictions, the SAE also occurred in the stripe rotation condition; yet surprisingly, the SAE was absent in the object rotation condition. This finding is surprising because the two rotation conditions were visually identical to the disoriented participant. A paired sample t-test indicated that participants might have oriented with respect to the landmarks and therefore presence for the SAE was tested for the 0˚ and 180˚ imagined perspectives in the object rotation condition. While physically facing 90˚ and with 0˚ as the body aligned perspective and 180˚ as the body misaligned perspective, there was not a significant difference in pointing error between body aligned

(*M* = 49.84, *SD* = 30.23) and body misaligned (*M* = 47.44, *SD* = 27.82), *t*(15) = .25, *p* = .806, d_{av} = .08, Hedges's g_{av} = .08. On average, body aligned responses were 2˚ higher than body misaligned (95% CI [-18.04 – 22.84]). However, while physically facing 270˚ and with 0˚ as the body misaligned perspective and 180˚ as the body aligned perspective, there was a numerical but non-significant difference in pointing error between body aligned (*M* = 38.25, *SD* = 21.16) and body misaligned (*M* = 60.84, *SD* = 42.85), *t*(15) = 2.00, *p* = .063, d_{av} = .67, Hedges's g_{av} = .64. On average, body misaligned responses were 23˚ higher than body aligned (95% CI [-1.38 – 46.54]). These results indicate that there was a trend towards facilitated performance for body aligned in alternate imagined perspectives in the object rotation condition (see Figure 9).

Four paired sample t-tests were calculated to compare body aligned, and body misaligned absolute pointing error in each test VE (see Figure 10). It was predicted that the SAE would be present in the no change condition and the object substitution condition but not in the object rotation or stripe rotation conditions. The results demonstrated that a SAE for the 90˚ and 270˚ perspectives was present in the no change, object substitution, and stripe rotation conditions. In the no change condition, there was a significant difference in absolute pointing error between body aligned (*M* = 38.72, *SD* = 12.97) and body misaligned (*M* = 54.47, *SD* = 24.82), *t*(15) = 2.81, *p* = .013, d_{av} = .80, Hedges's g_{av} = .75. On average, body misaligned errors were 16˚ higher than body aligned (95% CI [3.78 – 27.73]). In the object substitution condition, there was a significant difference in absolute pointing error between body aligned (*M* = 38.77, *SD* = 11.94) and body misaligned (*M* = 49.54, *SD* = 24.36), *t*(14) = 2.84, *p* = .013, d_{av} = .56, Hedges's g_{av} = .53. On average, body misaligned responses were 11˚ higher than body

aligned (95% CI [2.64 – 18.91]). In the stripe rotation condition, there was a significant difference in absolute pointing error between body aligned (*M* = 34.39, *SD* = 14.02) and body misaligned (*M* = 43.44, *SD* = 24.37), *t*(16) = 2.56, *p* = .021, d_{av} = .46, Hedges's g_{av} = .43. On average, body misaligned responses were nine degrees higher than body aligned (95% CI [1.55 – 16.57]). These results indicated that JRD performance was facilitated for perspectives aligned with the body (i.e., JRD errors were lower when the imagined facing direction matched the physical facing direction). In the object rotation condition, there was not a significant difference in absolute pointing error between body aligned (*M* = 47.16, *SD* = 18.82) and body misaligned (*M* = 46.29, *SD* = 18.24), *t*(15) = 0.30, *p* = .768, d_{av} = .05, Hedges's g_{av} = .04. On average, body misaligned responses were 0.88˚ lower than body aligned (95% CI [-7.09 – 5.34]).

Response latency followed a similar pattern to the absolute pointing error results (see Figure 11). In the no change condition, there was a significant difference in response time between body aligned (*M* = 8.33, *SD* = 1.73) and body misaligned (*M* = 9.90, *SD* = 2.01), *t*(15) = 3.45, *p* = .004, d_{av} = .84, Hedges's g_{av} = .79. On average, body misaligned response latency was 1.57 seconds longer than body aligned (95% CI [.60 – 2.53]). In the object rotation condition, there was not a significant difference in response time between body aligned (*M* = 8.77, *SD* = 2.11) and body misaligned (*M* = 9.28, *SD* = 3.20), *t*(15) = 0.79, *p* = .441, d_{av} = .19, Hedges's g_{av} = .18. On average, body misaligned response latency was .51 seconds longer than body aligned (95% CI [-.86 – 1.88]). In the stripe rotation condition, there was a significant difference in response time between body aligned (*M* = 8.04, *SD* = 2.16) and body misaligned (*M* = 9.55, *SD* = 3.17), *t*(16) = 2.40, *p* = .029, d_{av}, = .56, Hedges's g_{av} = .53. On average, body misaligned response latency was

1.51 seconds longer than body aligned (95% CI [.17 – 2.85]). In the object substitution condition, there was a significant difference in response time between body aligned (M = 7.33, SD = 1.36) and body misaligned (M = 8.70, SD = 2.05), $t(14) = 4.03$, $p = .001$, d_{av} = .79, Hedges's g_{av} = .75. On average, body misaligned response latency was 1.37 seconds longer than body aligned (95% CI [.64 – 2.10]).

Discussion

It was hypothesized that the SAE would occur when participants were tested in the no change and object substitution conditions, but the SAE would not occur in the object rotation or stripe rotation conditions. The results indicated that the SAE for pointing errors was present in almost all of the test VEs. These results suggest that participants regarded the test VEs similarly to the learning VE regardless of the spatial and non-spatial changes. One interpretation of this is that the spatial changes within the test VE failed to disrupt perceived self-location.

An explanation for the unpredicted results in the spatial change test VEs could be the relative saliency of the landmarks. Whereas the plant and cone were quite close to some of the small learned objects, the stripe on the wall was far from all the small objects. Participants may have paid more attention to the plant and cone during learning, and subsequently relied on those landmarks to reorient to the test VE. Under this scenario, the object rotation and stripe rotation conditions were not perceived as distinct from the learning VE because the conflict between the object and stripe cues went unnoticed or was ignored. Evidence for this was shown in the stripe rotation condition, in which there was a trend for the presence of the SAE for alternate perspectives (i.e., 0˚ and 180˚ imagined perspectives). Therefore, Experiment 2 modified the landmarks in an attempt to alter the relative salience.

CHAPTER 3. EXPERIMENT 2

The results of Experiment 1 demonstrated the SAE across almost all test VEs, including spatial change VEs. One possible explanation for the unexpected SAE in the spatial change VEs was over-reliance on the landmarks (e.g., plant and cone) compared to the blue stripe. Experiment 2 made two changes to the layout of the environment to alter the saliency of the landmarks and featural cues. First, the two landmarks (plant and cone) were located farther away from the center of the VE and the small object locations. Second, the room shape was altered from a circle to a rectangle. In Experiment 1 the VE resembled the environment Lenck-Santini et al. (2005) created. However, the methodological issues from Experiment 1 suggested that attention needed to be drawn to the surrounding room, and increasing room saliency was achieved by making the surrounding room rectangular.

A power analysis was conducted for Experiment 2 to estimate the appropriate sample size. G*Power (Version 3.1.9.2) was used to perform a power analysis, and the results revealed that for an 80% chance of detecting the effect size seen for the no change condition from Experiment 1 (d_{av} = 0.75), significant at the 5% level (one-tailed) a sample size of 15 would be required. Therefore, 16 participants per each condition were selected to keep sample size consistent from Experiment 1. Experiment 2 was pre-registered at the Open Science Framework (https://osf.io/qsbdc/).

Method

Participants

Eighty-nine undergraduate students from Iowa State University (F = 49) participated in exchange for course credit. To ensure that the changes to cue saliency

were effective, participants were assigned to the stripe rotation conditions first. After the target sample of 16 was achieved, the data were analyzed in the same manner as Experiment 1. As predicted, the SAE was not present for the stripe rotation condition which suggested that the changes to cue saliency were effective (see Results). Participants were then randomly assigned to the remaining conditions (no change, object rotation, and object substitution). Data from 25 participants (F = 21) were removed after outlier analysis (see Results). After outlier removal, additional participants were assigned to fill out the conditions that lost participant data. The final sample was 64 (F = 28), with the size of each condition as follows: no change condition (n = 16, F = 5), object rotation condition (n = 16, F = 9), stripe rotation condition (n = 16, F = 6), or object substitution condition (n = 16, F = 8). Gender was approximately balanced across conditions.

Stimuli and Design

The stimuli and design of Experiment 2 were identical to that of Experiment 1 with two modifications. First, the room shape was made rectangular (11.4m x 20m x 7.5m). Second, the landmarks (e.g., plant and cone) were placed closer to the walls in both VEs (i.e., both landmarks were located 5m away from the center of the VE compared to 2.5m from Experiment 1). The test conditions remained the same from Experiment 1 (see Figures 12 and 13).

Results

The protocol for excluding outliers remained the same from Experiment 1. There were 25 cases, eight (F = 8) from the no change, four (F = 3) from the object rotation, five (F = 4) from the stripe rotation, and seven (F = 6) from the object substitution condition, that did not significantly differ from chance performance and the data were not included in the following analyses. There was no evidence of a speed-accuracy tradeoff.

The within-participant correlation between pointing error and response latency was significantly positive (M = .16, SE = .07), $t(63) = 2.16$, p = .034. Pointing error was more responsive to the independent variables, though response latency generally supported the same conclusions, and so the focus is on pointing error.

Four paired sample t-tests were calculated to compare body aligned, and body misaligned absolute pointing error in each test VE (see Figure 15). It was predicted that the SAE would be present in the no change condition and the object substitution condition but not in the object rotation or stripe rotation conditions. The results demonstrated that a SAE for the 90˚ and 270˚ perspectives was present in the no change, object substitution, and object rotation conditions. In the no change condition, there was a significant difference in absolute pointing error between body aligned (M = 49.82, SD = 14.99) and body misaligned (M = 65.80, SD = 26.39), $t(15) = 2.83$, p = .013, d_{av} = .75, Hedges's g_{av} = .71. On average, body misaligned errors were 16˚ higher than body aligned (95% CI [3.83 – 28.03]). In the object substitution condition, there was a significant difference in absolute pointing error between body aligned (M = 46.74, SD = 14.07) and body misaligned (M = 57.94, SD = 20.11), $t(15) = 3.23$, p = .006, d_{av} = .65, Hedges's g_{av} = .61. On average, body misaligned responses were 11˚ higher than body aligned (95% CI 3.81 – 18.60]). In the object rotation condition, there was a significant difference in absolute pointing error between body aligned (M = 51.44, SD = 13.80) and body misaligned (M = 65.93, SD = 16.62), $t(15) = 4.50$, $p < .001$, d_{av} = .95, Hedges's g_{av} = .90. On average, body misaligned responses were 14˚ higher than body aligned (95% CI [7.62 – 21.36]). These results indicated that JRD performance was facilitated for perspectives aligned with the body. In the stripe rotation condition, there was not a

significant difference in absolute pointing error between body aligned (M = 54.01, SD = 20.21) and body misaligned (M = 54.38, SD = 17.85), $t(15) = 0.150$, $p = 0.883$, d_{av} = .02, Hedges's g_{av} = .02. On average, body misaligned responses were 0.37˚ higher than body aligned (95% CI [-4.90 – 5.64]).

Response latency followed a similar pattern to the absolute pointing error results, except for the object rotation condition (see Figure 15). In the no change condition, there was a significant difference in response time between body aligned (M = 7.30, SD = 1.67) and body misaligned (M = 8.30, SD = 1.74), $t(15) = 3.71$, $p = .002$, d_{av} = .59, Hedges's g_{av} = .56. On average, body misaligned response latency was .99 seconds longer than body aligned (95% CI [.42 – 1.56]). In the object rotation condition, there was not a significant difference in response time between body aligned (M = 7.49, SD = 2.05) and body misaligned (M = 8.02, SD = 2.16), $t(15) = 1.46$, $p = .166$, d_{av} = .25, Hedges's g_{av} = .24. On average, body misaligned response latency was .53 seconds longer than body aligned (95% CI [-.25 – 1.31]). In the stripe rotation condition, there was not a significant difference in response time between body aligned (M = 8.44, SD = 2.62) and body misaligned (M = 8.73, SD = 2.82), $t(15) = .74$, $p = .470$, d_{av} = .11, Hedges's g_{av} = .10. On average, body misaligned response latency was .30 seconds longer than body aligned (95% CI [-.55 – 1.15]). In the object substitution condition, there was a significant difference in response time between body aligned (M = 8.06, SD = 2.25) and body misaligned (M = 8.98, SD = 2.10), $t(15) = 2.43$, $p = .028$, d_{av} = .42, Hedges's g_{av} = .40. On average, body misaligned response latency was .93 seconds longer than body aligned (95% CI [.11 – 1.74]).

Discussion

In Experiment 2, an attempt was made to change the cue salience from Experiment 1. Participant performance was tested to see if these changes in cue salience were effective by examining responses in the stripe rotation condition. In Experiment 1, the stripe rotation condition exhibited the SAE which was not predicted based on the results from Lenck-Santini et al. (2005). Therefore, this condition was a great candidate to test whether the changes made to the environment had the intended effect. As predicted from Experiment 1 and 2, the SAE was not present for the stripe rotation condition which suggested that the changes made to the environment did alter saliency in the expected direction.

The remaining hypotheses for Experiment 2 were the same from Experiment 1, and the results generally followed the predictions. As predicted, the SAE was present for pointing errors in the no change and object substitution condition, and the SAE was absent for pointing errors in the stripe rotation condition. However, the SAE was also present for pointing errors in the object rotation condition. This result is surprising given that the object rotation and stripe rotation condition were visually identical to the participant upon exploration of the VE.

An explanation for this unexpected result may be the participant's view during testing. In the stripe rotation condition, the participant faced conflicting stimuli while performing JRDs. Specifically, when the participant was physically facing 270˚ during testing, the cone and blue wall were both centered in the participant's view; when the participant was physically facing 90˚ during testing, the wall behind the plant was further away from the participant than it was during learning. These two test views were never

seen during learning and served as a continual reminder of the spatial change that occurred before testing.

Conversely, in the object rotation condition, the participant only faced the walls of the VE, with the landmarks and featural cue out of view during testing. The continuous presentation of conflicting stimuli in the stripe rotation VE may have influenced responses during testing and reminded the participant that the occupied VE was different from the learning VE. Recent work has shown that the SAE was present, albeit it to a lesser effect, in test environments that differed (i.e., larger room scale and appearance), but still preserved, other aspects of the learning environment (e.g., room shape) (Riecke & McNamara, 2017). These results appear conceptually similar to partial remapping where only a select number of rodent place cells remap when introduced to an altered environment. Additionally, single-cell recording in epileptic patients has revealed a dissociation between place- and view-responsive cells within the hippocampus and parahippocampal region respectively (Ekstrom et al., 2003). Place-responsive cells fired robustly when the participant was in specific spatial locations, whereas view-responsive cells fired robustly when the participant viewed specific landmarks independent of spatial location. These findings suggest that specific views during a navigation task (e.g., landmarks) also play an essential role in the formation of map-like representations of space (O'Keefe & Nadel, 1978). In the current experiment, the lack of continual presentation of conflicting cues in the object rotation condition may have reduced participant awareness of the spatially changed VE, as opposed to the continual presence in the stripe rotation condition, and therefore increased the probability for SAE presence.

It is also important to note that the number of outliers (n = 25) was much higher in Experiment 2 compared to Experiment 1 (n = 7). This could have been due to changes in the VE across experiments, particularly in moving the landmarks farther away from the small objects in the learning VE of Experiment 2. Although the learning criterion (three repetitions of walking to the location of each object followed by feedback) was preserved from Experiment 1, a better alternative may be to have an objective criterion for learning object location. For example, instead of the experimenter subjectively determining how close a participant's judgment was to the small object location, a distance threshold could be implemented in the VE. This threshold could record, in meters, how close the participant's response is to the actual object location. To determine sufficient learning, a participant would have to be within a predetermined distance of the object for several consecutive trials. This method for learning would then serve as a more objective measure of learning and therefore reduce data loss due to unusually high errors.

Experiment 2 indicates that human perception of self-location may be influenced by neural mechanisms similar to the rodent place cell system. For example, in non-spatial change conditions (e.g., no change and object substitution conditions) the SAE was present, which suggests that participant's perception of self-location was influenced by the spatial layout of the learning VE. Additionally, manipulations that disrupted rodent place cells (e.g., spatial changes) also affected human perception of self-location, as demonstrated by no SAE in the stripe rotation condition. However, it also appears that conflicting perceptual input during testing influences human perception of self-location. In the object rotation condition, the SAE was present, and this result was unexpected since the object rotation, and stripe rotation condition was visually identical. An

explanation for this surprising result may be what the participant viewed during testing (i.e., continual presentation of a cue conflict).

A planned follow-up study will examine how conflicting perceptual input affects SAE presence/absence during testing. This proposed experiment will use the cue rotation condition from Experiment 2 that did not show the SAE (i.e., the stripe rotation condition) and will have participants face two directions during testing. One facing direction will present a featural cue conflict represented by the cone in front of the blue wall (Figure 16, lower left panel), which will serve as a continual reminder during testing that the environment is not identical to the learning environment. The other facing direction will not present a visual conflict during testing, as the participant will be facing only a blank uncolored wall with no landmarks visible (a view that could occur even when standing in the learning VE, such as when facing 180 degrees or after sidestepping to the left or right of a landmark object; Figure 16, lower-right panel). The expectation is that if the SAE is influenced by conflicting perceptual input during retrieval, then the SAE may not be present for the facing direction that has a cue conflict since there is a continual presentation that the test environment is dissimilar to the learning environment. For the facing direction that does not have a cue conflict, the SAE may be present since there is no visual cue that alerts the participant to the novel environment. This follow-up experiment will examine how landmarks and featural cue conflicts influence individuals' perception of self-location via the presence/absence of the SAE.

CHAPTER 4. GENERAL DISCUSSION

Place cell firing occurs when features of occupied space, such as room shape and visual cues, drive place cells to attain a critical value or threshold that allow for firing to occur (Muller & Kubie, 1987). Additionally, place cell firing appears to not only represent locations within an environment but also represent multiple, distinct spaces via the process of remapping. While the location of remapped place cells cannot reliably be predicted by researchers (i.e., unclear where, or if, a particular place cell will fire in a novel environment), it is suggested that the locations of place cells in novel environments function similarly. Hence when changes occur in an environment (e.g., altered room shape), place cell firing can change by shifting field position or by changing firing rate (i.e., activate previously silent place cells) (Anderson & Jeffrey, 2003; O'Keefe & Conway, 1978; Wills, Lever, Cacucci, Burgess, & O'Keefe, 2005). This phenomenon of remapping has been demonstrated under several conditions, such as in darkness (Quirk, Muller, & Kubie, 1990), with different environmental colors and scents (Anderson & Jeffery, 2003), and across 11 distinct environments (Alme et al., 2014).

Though most prior research on place cells used single-cell recordings in animals, place-responsive cells have been identified in the human hippocampus (Ekstrom et al., 2003), as well as remapping-like spatial representations (Steemers et al., 2016). Therefore, investigations into these shared properties using human behavior studies could strengthen these findings, especially given the challenges associated with conducting neuroscientific research on human place cells (e.g., invasive techniques, limited mobility, etc.).

In the current study, the focus was on the observation that rodent place cells partially remap after spatial environmental changes (rotating objects relative to enclosure) but are unaffected by non-spatial changes (object substitution) (Lenck-Santini et al., 2005). Experiment 1 and 2 predicted similar findings using the SAE as a proxy for perceived self-location. It was hypothesized that if the spatial arrangement was not disrupted from the learning VE (e.g., no change and object substitution condition), the SAE would be present. This presence would indicate that the participants believed he or she was in an environment that resembled the learning VE. However, if the spatial arrangement was disrupted from the learning VE (e.g., object and stripe rotation condition), then the SAE would be absent. This absence would indicate that the participant believed he or she was located in an environment distinct from the learning VE.

As predicted, in Experiment 1, the SAE was present when the spatial arrangement was preserved (no change and object substitution). Contrary to predictions, in Experiment 1 the SAE was also present for the stripe rotation and object rotation VE (for object rotation, the advantage was for 0° and 180° perspective). These results were surprising as the object and stripe rotation conditions were visually identical. A possible explanation for the unexpected SAE in the spatial change VEs was an over-reliance on the landmarks (plant and cone) compared to the featural cue (blue stripe on the wall) which may have created differences in cue salience during learning. Therefore, an attempt was made to decrease landmark saliency by placing the plant and cone further away from the small learned objects and increase featural cue saliency by changing the geometry of the VEs from circular to rectangular.

These changes to cue saliency appeared to resolve the methodological issues in Experiment 1 as evidenced by the absence of the SAE for the stripe rotation condition (a condition that previously demonstrated a SAE). Additionally, the results from Experiment 2 were in the predicted direction for the non-spatial change environments, since the SAE was present in both the no change and object substitution conditions. However, the SAE was also present in the object rotation condition. This result was surprising given that the object and stripe rotation conditions were visually identical. An explanation for this difference could be attributed to participant view during testing. In the stripe rotation condition, participants were continually presented with a cue conflict (i.e., a view never seen during learning) which may have served as a reminder that the current environment was different from the learning VE. In the object rotation condition, participants did not view a cue conflict during testing. Instead, participants viewed the walls of the inhabited VE, a view that was seen during testing. These differences in participant view during testing may have influenced participants' perception of self-location, and a follow-up study examining conflicting stimuli during test will attempt to clarify the discrepancy in results between conditions.

Although most prior research on place cells used single-cell recordings in animals, research with humans seems to corroborate these findings. For example, studies have identified place-responsive cells (Ekstrom et al., 2003) and remapping-like properties (Steemers et al., 2016) in the human hippocampus. Converging evidence from human behavioral experiments strengthen these findings, especially given the challenges associated with conducting neuroscientific research on human place cells in humans (e.g., human single-cell recording studies are rare, and neuroscience research on humans

almost always involves immobile participants). The current study explored the effect of environmental manipulations on human perceived self-location, and these experiments, especially Experiment 2, suggest that human perception of self-location appears to be influenced by similar manipulations that either disrupt (e.g., spatial changes) or do not disrupt (e.g., non-spatial changes) rodent place cells. However, conclusions from these results are limited in that this behavioral design makes inferences about place-responsive activity (since there were no direct recordings). Additional evidence is needed in order to establish that spatial environmental cues cause disruptions in perceived self-location via place-responsive remapping.

These results also extend our understanding of the mechanisms that influence the SAE, since the SAE was present and absent in two environments that were visually similar to disoriented participants. The only difference between the two environments was participant view during testing. This result suggests that what a participant sees during testing may influence the presence/absence of the SAE, and future investigations should examine how conflicting stimuli influence perceived self-location. Overall, the current study helps to expand our understanding of the mechanisms that influence human perception of self-location and strengthen the findings from fMRI studies that identified place-responsive cells (Ekstrom et al., 2003) and remapping-like properties (Steemers et al., 2016) in the human hippocampus.

REFERENCES

Alme, C. B., Miao, C. M., Jezek, K., Treves, A., Moser, E. I., & Moser, M. B. (2017). Place cells in the hippocampus: Eleven maps for eleven rooms. *PNAS, 111*(52), 18428-18435.

Anderson, M. I. & Jeffrey, K. J. (2003). Heterogenous modulation of place cell firing by changes in context. *The Journal of Neuroscience, 23*(26), 8827-8835.

Barry, C., Hayman, R., Burgess, N., & Jeffrey, K. J. (2007). Experience-dependent rescaling of entorhinal grid cells. *Nature Neuroscience,* 1-3.

Boccara, C. N., Sargolini, F., Thoresen, V. H., Solstad, T., Witter, M. P., Moser, E. I., & Moser, M. B. (2010). Grid cells in pre- and parasubiculum. *Nature Neuroscience, 13*(8), 987-997.

Chen, X., He, Q., Kelly, J. W., Fiete, I. R., & McNamara, T. P. (2015). Bias in human path integration is predicted by properties of grid cells. *Current Biology, 25,* 1771-1776.

Eichenbaum, H. (2017). The role of the hippocampus in navigation is memory. *J Neurophsyiol., 117,* 1785-1796.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Ishan, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature, 425,* 184-187.

Fox, N. C., Warrington, E. K., Freeborough, P. A., Hartikaninen, P., Kennedy, A. M., Stevens, J. M., & Rossor, M. N. (1996). Presymptomatic hippocampal atrophy in Alzheimer's disease: A longitudinal MRI study. *Brain, 119,* 2001-2007.

Grieves, R. M. & Jeffery, K. J. (2017). The representation of space in the brain. *Behavioural Processes, 135,* 113-131.

Hartley, T., Lever, C., Burgess, N., & O'Keefe, J. (2014). Space in the brain: How the hippocampal formation supports spatial cognition. *Phil. Trans. R. Soc. B., 369,* 1-18.

Hori, E., Nishio, Y., Kazui, K., Umeno, K., Tabuchi, E., Sasaki, K., …Nishijo, H. (2005). Place-related neural responses in the monkey hippocampal formation in virtual space. *Hippocampus, 15,* 991-996.

Kelly, J. W., Avraamides, M. N., Loomis, J. M. (2007). Sensorimotor alignment effects in the learning environment and in novel environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33*(6), 1092-1107.

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Gollege, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion. *Psychological Science, 9*(4), 293-298.

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. *Frontiers in Psychology, 4*(863), 1-12.

Lenck-Santini, P. P., Rivard, B., Muller, R. U., & Poucet, B. (2005). Study of CA1 place cell activity and exploratory behavior following spatial and nonspatial changes in the environment. *Hippocampus, 15,* 356-369.

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science, 280,* 921-924.

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the 'cognitive map.' *Nature Reviews: Neuroscience, 7,* 663-678.

Miller, J. F., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, I., … Hefft, S. (2013). Neural activity in the human hippocampal formation reveals the spatial context of retrieved memories. *Science, 342,* 1111-1114.

Moser, M. B., Rowland, D. C. & Moser, E. I. (2015). Place cells, grid cells, and memory. *Cold Spring Harbor Perspective Biol., 7*(2), 1-15.

Muller, R. U. & Kubie, J. L. (1987). The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *The Journal of Neuroscience, 7*(7). 1951-1968.

Muller, R. U., Ranck, J. B., Taube, J. S. (1996). Head direction cells: Properties and functional significance. *Current Opinion in Neurobiology, 6,* 196-206.

O'Keefe, J. (1979). A review of the hippocampal place cells. *Progress in Neurobiology, 13,* 419-439.

O'Keefe, J. & Conway, D. H. (1978). Hippocampal place units in the freely moving rat: Why they fire where they fire. *Experimental Brain Research, 31,* 573-590.

O'Keefe, J. & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research, 34,* 171-175.

O'Keefe, J. & Nadel, L. (1978). *The Hippocampus as a Cognitive Map.* Oxford, England: Oxford University Press.

Park, E., Dvorak, D., & Fenton, A. A. (2011). Ensemble place codes in hippocampus: CA1, CA3, and dentate gyrus place cells have multiple place fields in large environments. *PLOS One, 6*(7), 1-9.

Poucet, B., Chapus, N., Durup, M., & Thinus-Blanc, C. (1986). A study of exploratory behavior as an index of spatial knowledge in hamsters. *Animal Learning & Behavior, 14*(1), 93-100.

Quirk, G. J., Muller, R. U., & Kubie, J. L. (1990). The firing of hippocampal place cell sin the dark depends on the rat's recent experience. *The Journal of Neuroscience, 10*(6), 2008-2017.

Riecke, B. E. & McNamara, T. P. (2017). Where you are affects what you can easily imagine: Environmental geometry elicits sensorimotor interference in remote perspective taking. *Cognition, 169,* 1-14.

Ruddle, R. A. & Lessels, S. (2006). For efficient navigational search, humans require full physical movement, but not a rich visual scene. *Psychological Science, 17*(6), 460-465.

Save, E., Poucet, B., Foreman, N., & Buhot, M. C. (1992). Object exploration and reactions to spatial and nonspatial changes in hooded rats following damage to parietal cortex or hippocampal formation. *Behavioral Neuroscience, 106*(3), 447-456.

Scoville, W. B. & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiat., 20*(11), 11-21.

Solstad, T., Moser, E. I., & Einevoll, G. T. (2006). From grid cells to place cells: A mathematical model. *Hippocampus, 16,* 1026-1031.

Spiers, H. J., Maguire, E. A., Burgess, N. (2001). Hippocampal amnesia. *Neurocase, 7,* 357-382.

Steemers, B., Vicente-Grabovetsky, A., Barry, C., Smulders, P., Schröder, T. N., Burgess, N., & Doeller, C. F. (2016). Hippocampal attractor dynamics predict memory-based decision making. *Current Biology, 26,* 1750-1757.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990a). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *The Journal of Neuroscience, 10*(2), 420-435.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990b). Head-direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations. *The Journal of Neuroscience, 10*(2), 436-447.

Thinus-Blanc, C., Bouzouba, L., Chaix, K., Chapuis, N., Durup, M., & Poucet, B. (1987). A study of spatial parameters encoded during exploration in hamsters. *Journal of Experimental Psychology: Animal Behavior Processes, 13*(4), 418-427.

Thompson L. T. & Best, P. J. (1990). Long-term stability of the place-field activity of single units recorded from the dorsal hippocampus of freely behaving rats. *Brain Research, 509*(2), 299-308.

Tolman, E. C. (1948). Cognitive maps in rats and me. *The Psychological Review, 55*(4), 189-208.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. I. Orientation and the short-cut. *Journal of Experimental Psychology, 36*(1), 13-24.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A. Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science, 277,* 376-380.

Wehner, R. (2003). Desert ant navigation: How miniature brains solve complex tasks. *J Comp Physiol, 189,* 579-588.

Williams, B., Narasimham, G., Westerman, C., Rieser, J., & Bodenheimer, B. (2007). Functional similarities in spatial representations between real and virtual environments. *ACM Transactions on Applied Perception, 4*(2), 1-20.

Wills, T. J., Lever, C., Cacucci, F., Burgess, N., & O'Keefe, J. (2005). Attractor dynamics in the hippocampal representation of the local environment. *Science, 308*(5723), 873-876.

Wolbers, T. & Hegarty, M. (2010). What determines our navigational abilities? *Trends in Cognitive Science, 14*(3), 138-146.

FIGURES

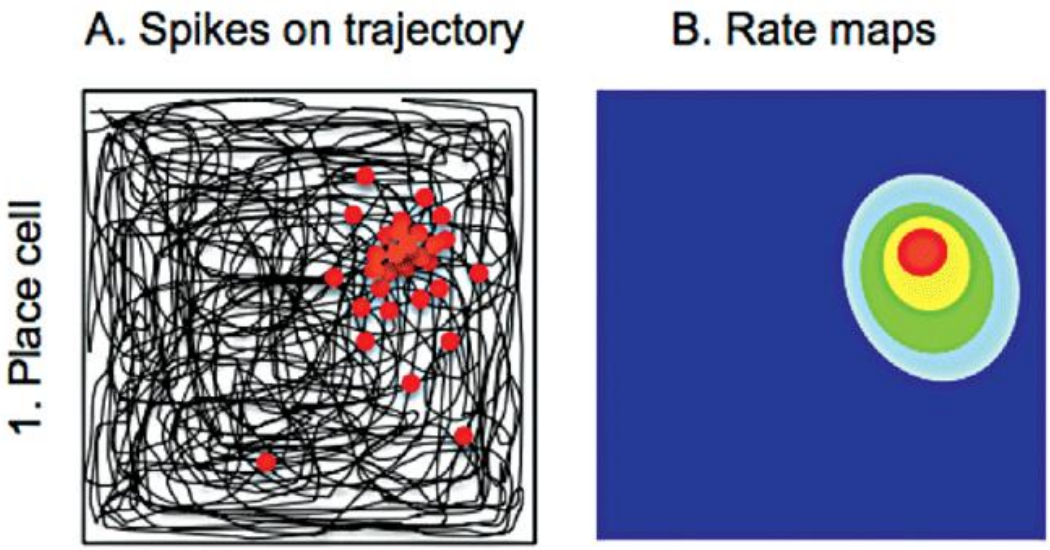


Figure 1. Schematic of place cell firing adapted from Moser, Rowland, & Rowland (2015) Figure 1. Column A shows (in black) the path taken by a rat as it traverses a square environment. Electrodes implanted in the hippocampus and entorhinal cortex record individual neurons. Place cells show increase firing (red dots signify action potentials) at discrete locations in the environment. Column B shows firing frequency with lower wavelength colors (yellow and red) depicting higher rates of firing on a background of silent activity (dark blue).

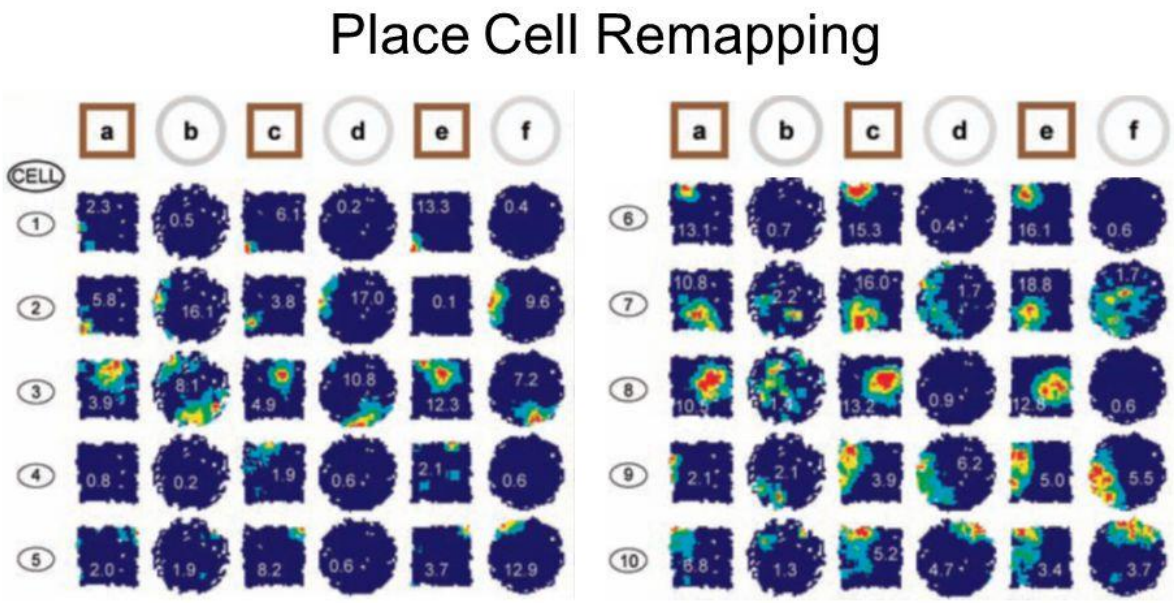


Figure 2. Environmental manipulations adapted from Wills, Lever, Cacucci, Burgess, & O'Keefe (2005) Figure 1. Example of a remapping across a brown plastic square box and a white wooden circle box. Cells 1-5 show increasing divergence between the two distinct environments, while cells 6-10 show differentiation from the beginning. Numbers show peak firing rate in hertz (Hz) to one decimal place.

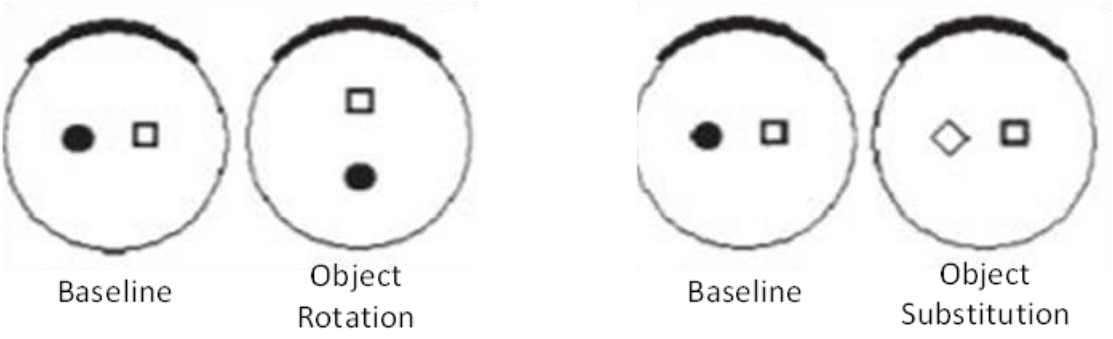


Figure 3. Environmental manipulations adapted from Lenck-Santini et al. (2005) Figure 1. Example of a spatial change in on the left (Object Rotation) and non-spatial change on the right (Object Substitution) from initial environment (Baseline).

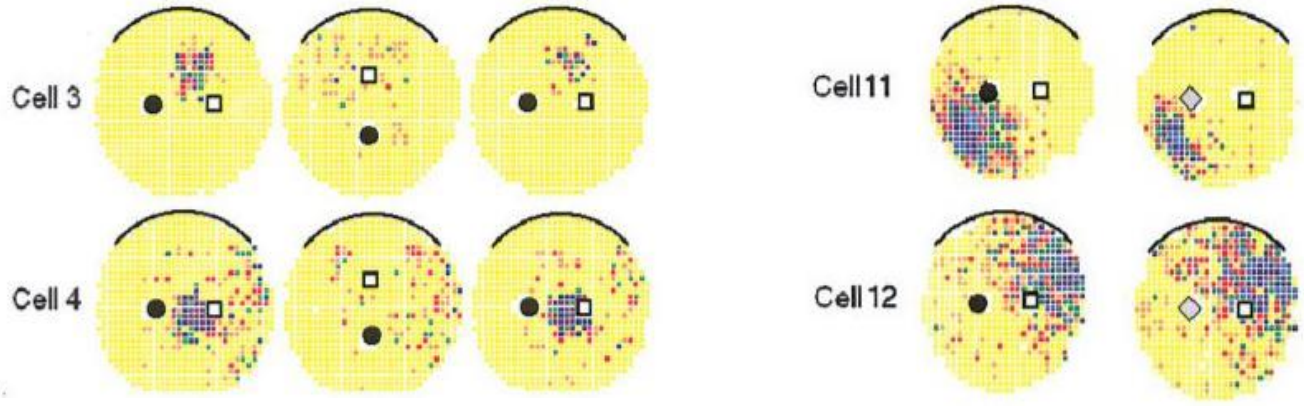


Figure 4. Varying effects of object rotation (left) and object substitution (right) from Lenck-Santini et al. (2005) Figure 4. The field of cell 3 and cell 4 were markedly changed after object rotation. Conversely, the field of cell 11 and cell 12 showed no obvious changes following object substitution. Color codes for each firing rate map were based on cell firing during the standard session. Median firing rates for colors: cell 3: yellow, 0.0; orange, 1.6; red, 2.6; green, 3.3; blue, 4.6; purple 6.4 AP/s; cell 4: 0.0; 0.8; 1.9; 3.2; 6.0; 14.7 AP/s; cell 11: 0.0; 0.8; 2.5; 4.3; 6.3; 11.6 AP/s; cell 12: 0.0; 1.2; 2.3; 3.6; 5.0; 7.6 AP/s.

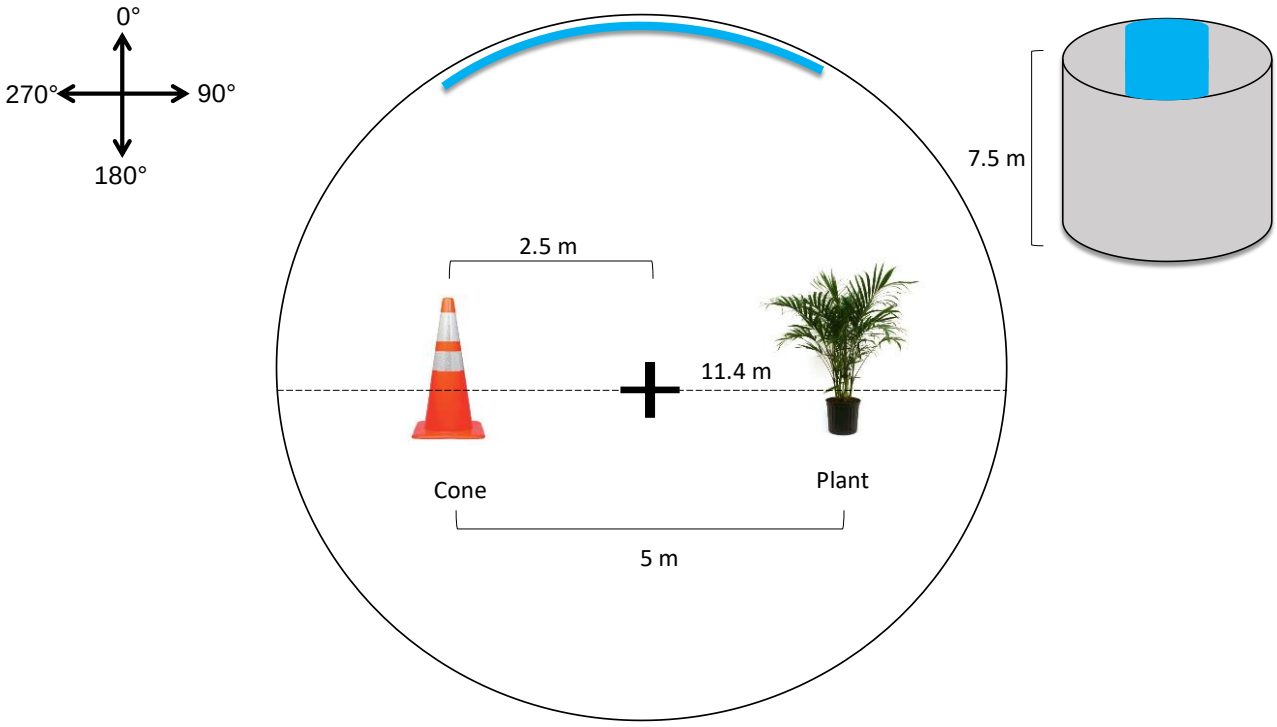


Figure 5. Layout of the learning VE from Experiment 1. Compass (top left) indicates experimenter-defined directions. Circular room (top right) is the VE.

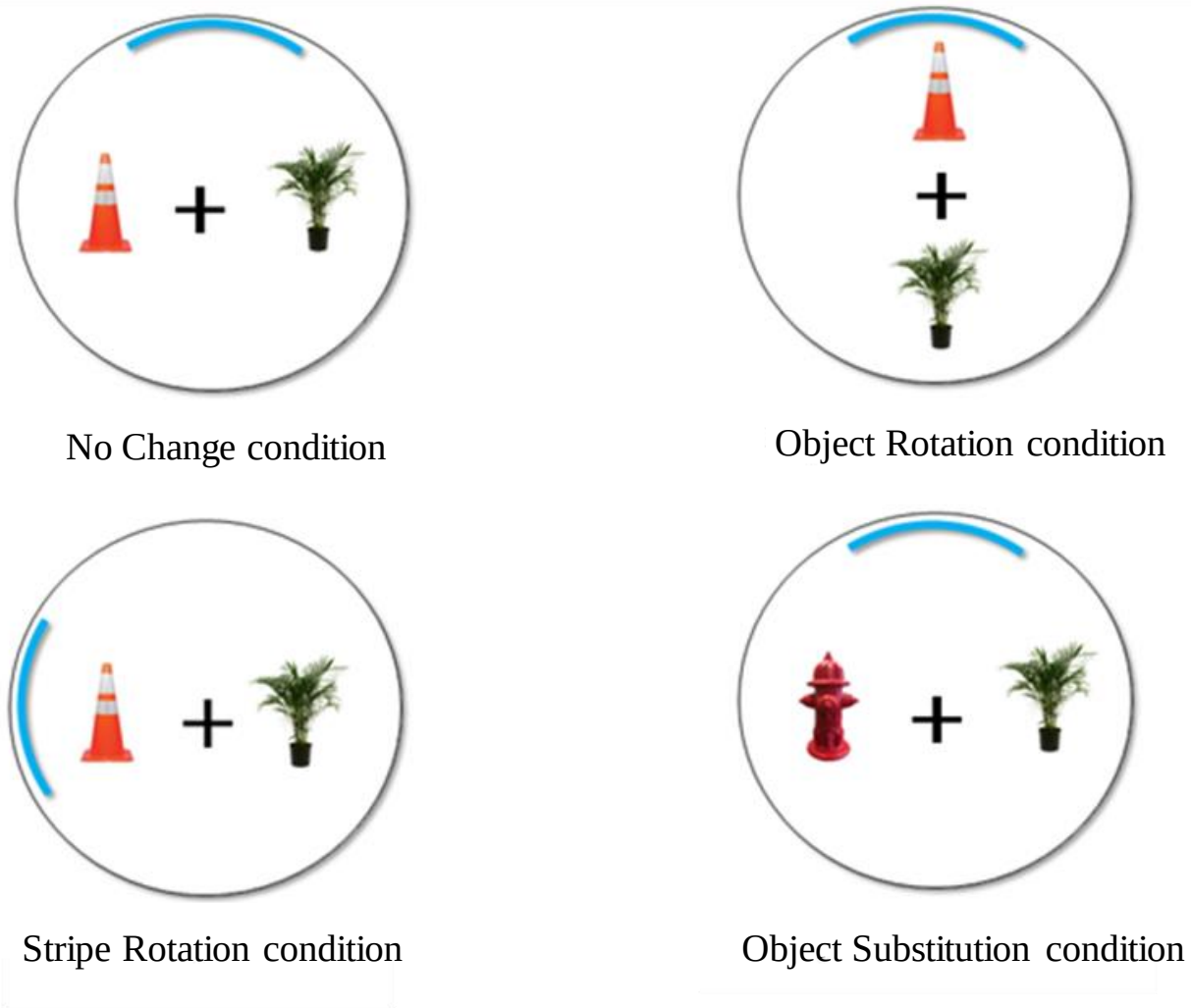
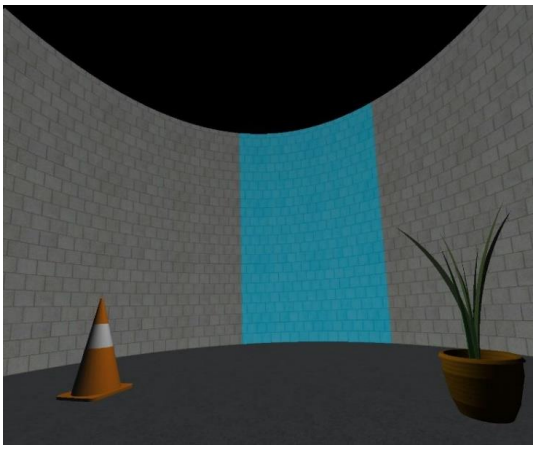
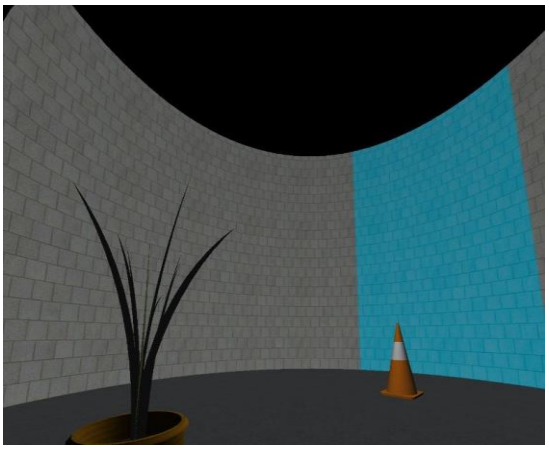


Figure 6. Schematic of the four test virtual environments (VEs) from Experiment 1. Clockwise, from top left, no change (identical to the learning VE), object rotation, object substitution, and stripe rotation condition.

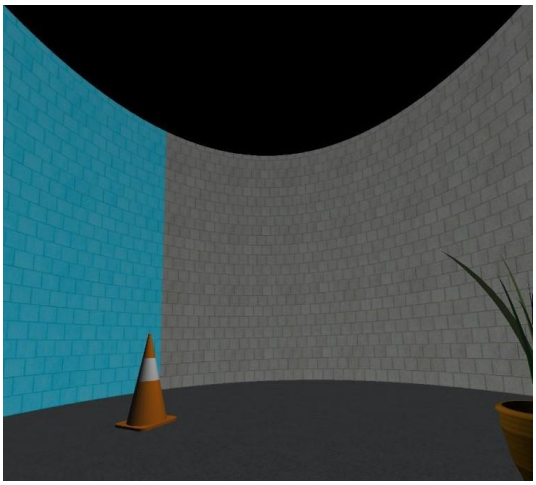


No Change condition

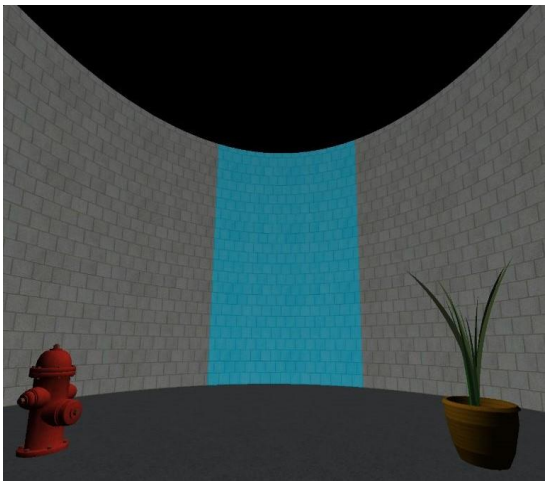
(same as Learning VE)



Object Rotation condition



Stripe Rotation condition



Object Substitution condition

Figure 7. Four test virtual environments (VEs) from Experiment 1. Clockwise, from top left, no change (identical to the learning VE), object rotation, object substitution, and stripe rotation condition.

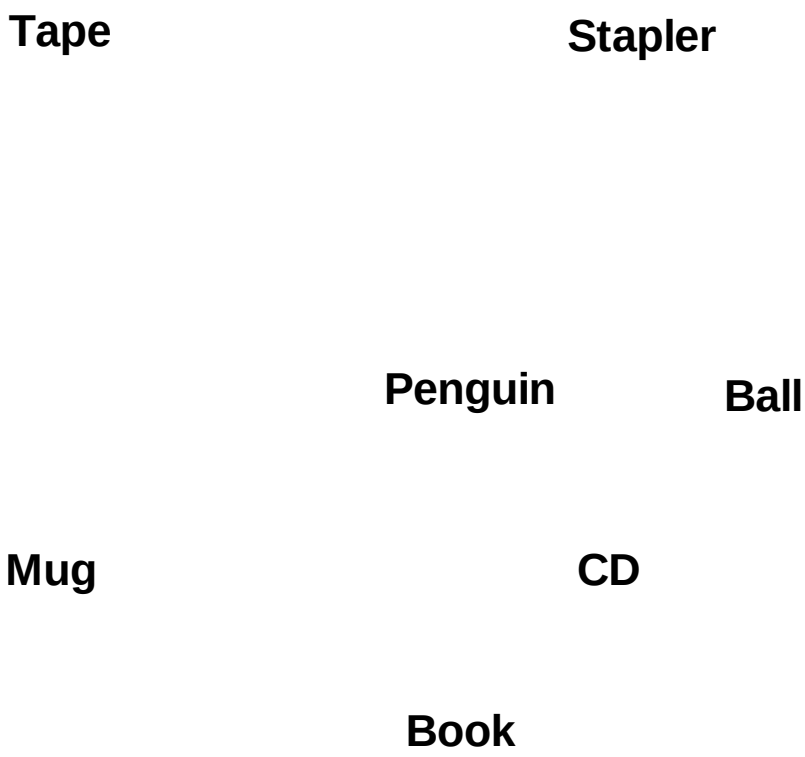


Figure 8. Layout of objects and corresponding locations that participants learned in the learning VE. Participants never saw all the objects in relation to each other.

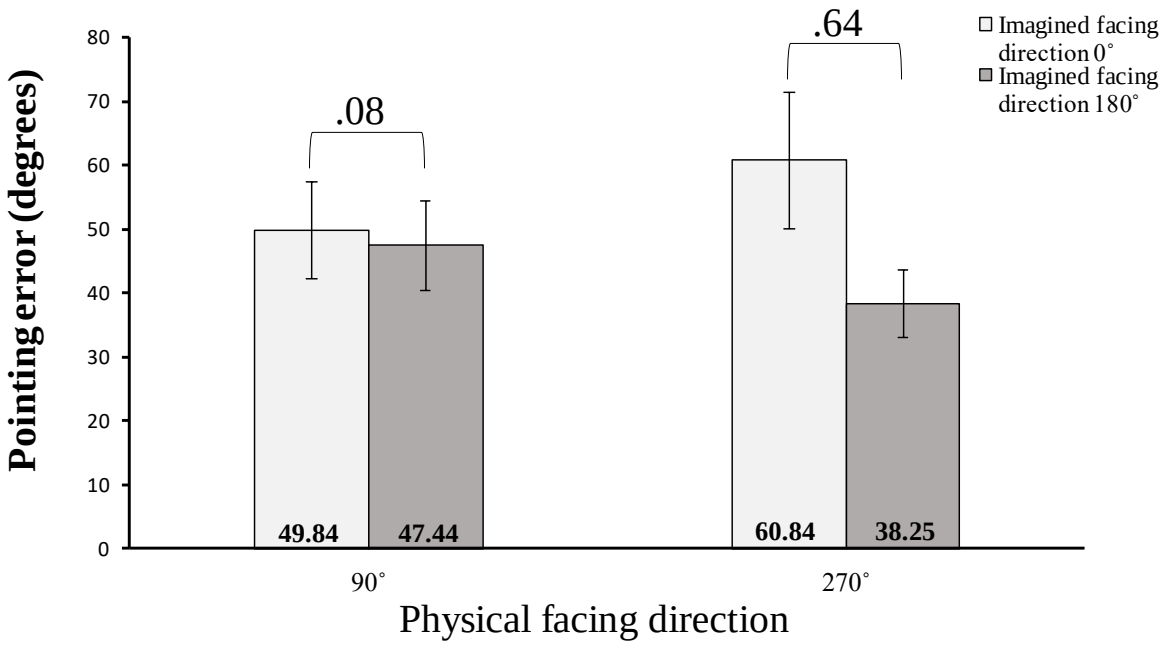


Figure 9. Average absolute pointing error (degrees) for the 0° and 180° imagined perspectives as a function proposed facing direction from the object rotation condition in Experiment 1. Error bars represent +/- 1 standard error. Effect size (in Hedge's $g_{average}$) is presented above the brackets.

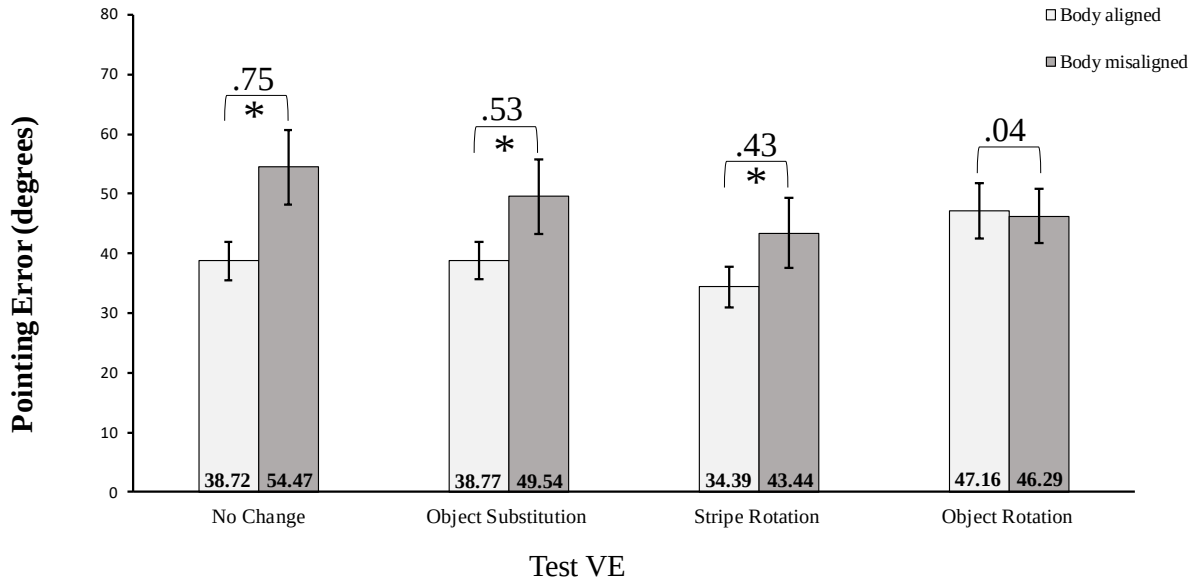


Figure 10. Average absolute pointing error (degrees) for the 90° and 270° imagined perspectives as a function of test environment from Experiment 1. Error bars represent +/- 1 standard error. Effect size (in Hedge's $g_{average}$) is presented above the brackets. *Note.* $*p < .05$

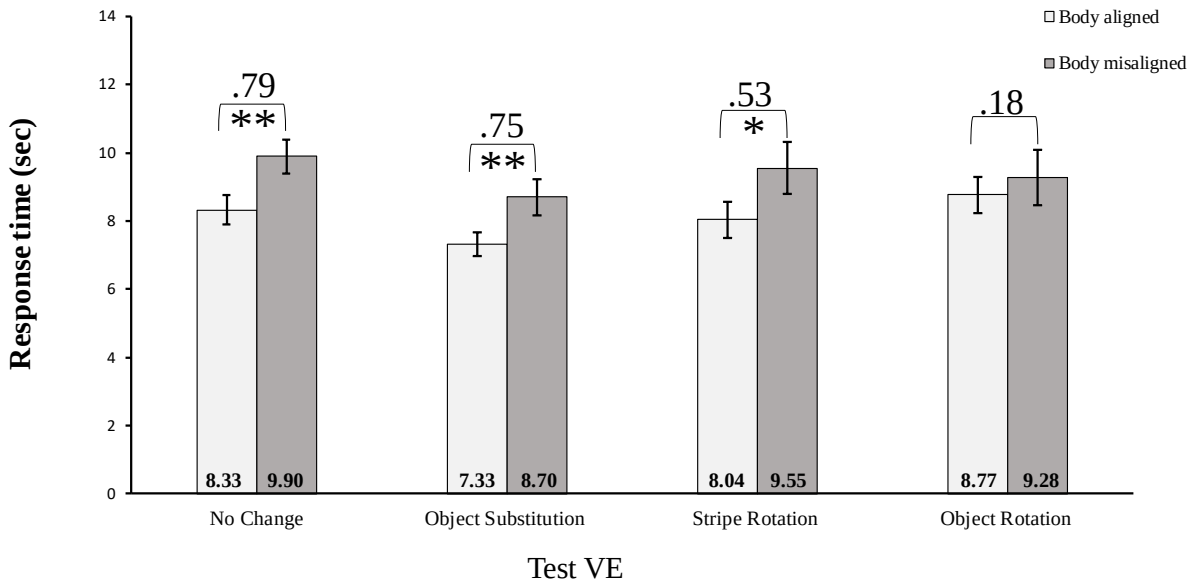
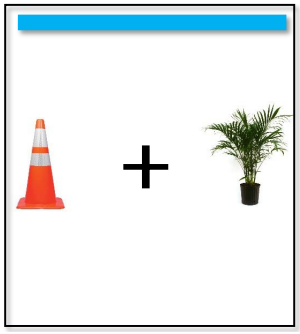
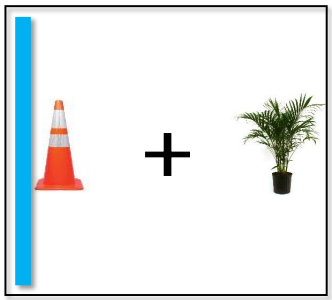


Figure 11. Response latency (sec) for the 90° and 270° imagined perspectives as a function of test environment from Experiment 1. Error bars represent +/- 1 standard error. Effect size (in Hedge's $g_{average}$) is presented above the brackets.
Note. **p* < .05, ***p* <.01



No Change condition
(same as Learning VE)

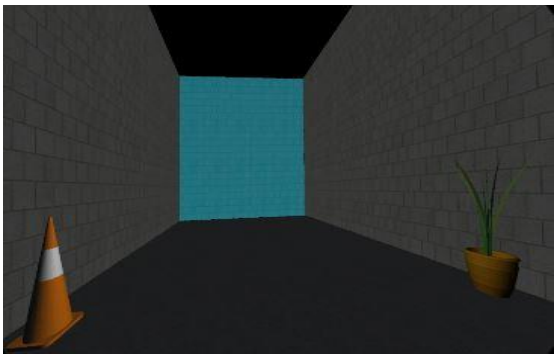
Object Rotation condition



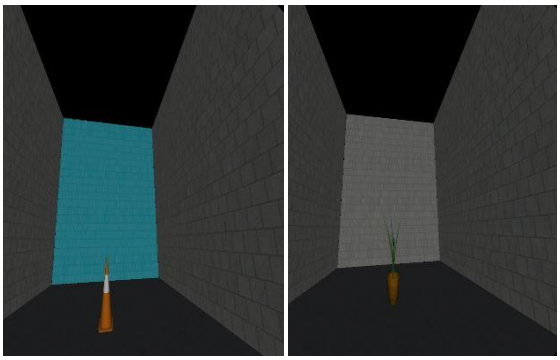
Stripe Rotation condition

Object Substitution condition

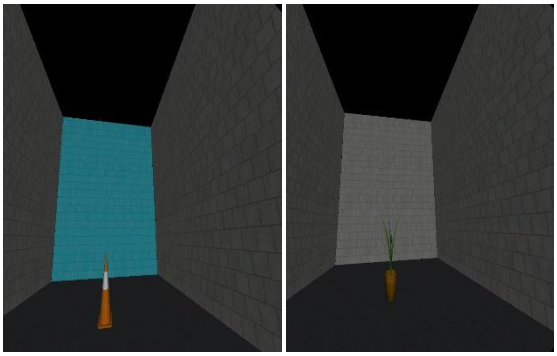
Figure 12. Schematic of the four test virtual environments (VEs) from Experiment 2. Clockwise, from top left, no change (identical to the learning VE), object rotation, object substitution, and stripe rotation condition.



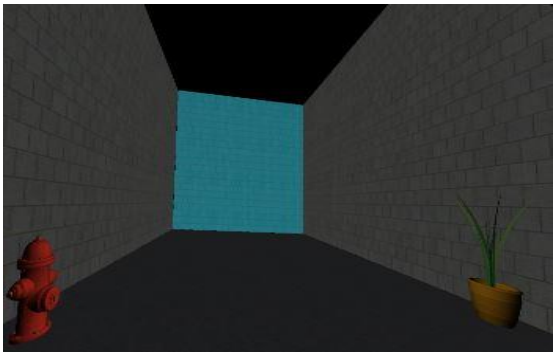
No Change condition
(same as Learning VE)



Object Rotation condition



Stripe Rotation condition



Object Substitution condition

Figure 13. Four test virtual environments (VEs) from Experiment 2. Clockwise, from top left, no change (identical to the learning VE), object rotation, object substitution, and stripe rotation condition.

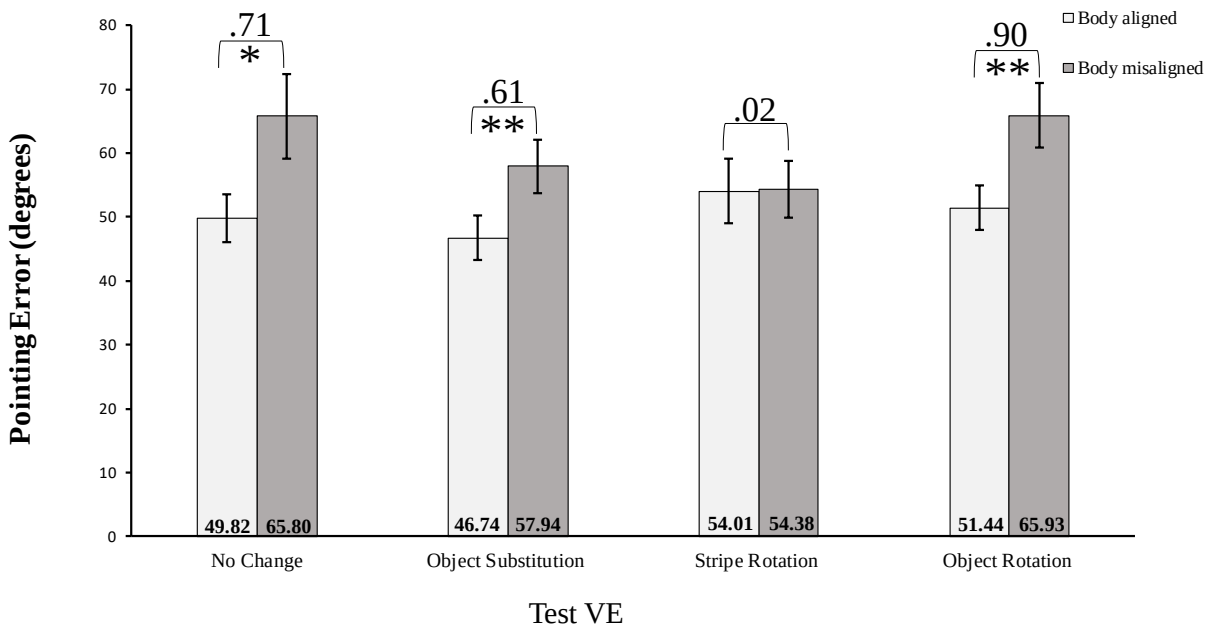


Figure 14. Absolute pointing error (degrees) for the 90° and 270° imagined perspectives as a function of test environment from Experiment 2. Error bars represent +/- 1 standard error. Effect size (in Hedge's $g_{average}$) is presented above the brackets.
Note. $*p < .05$, $** p < .01$

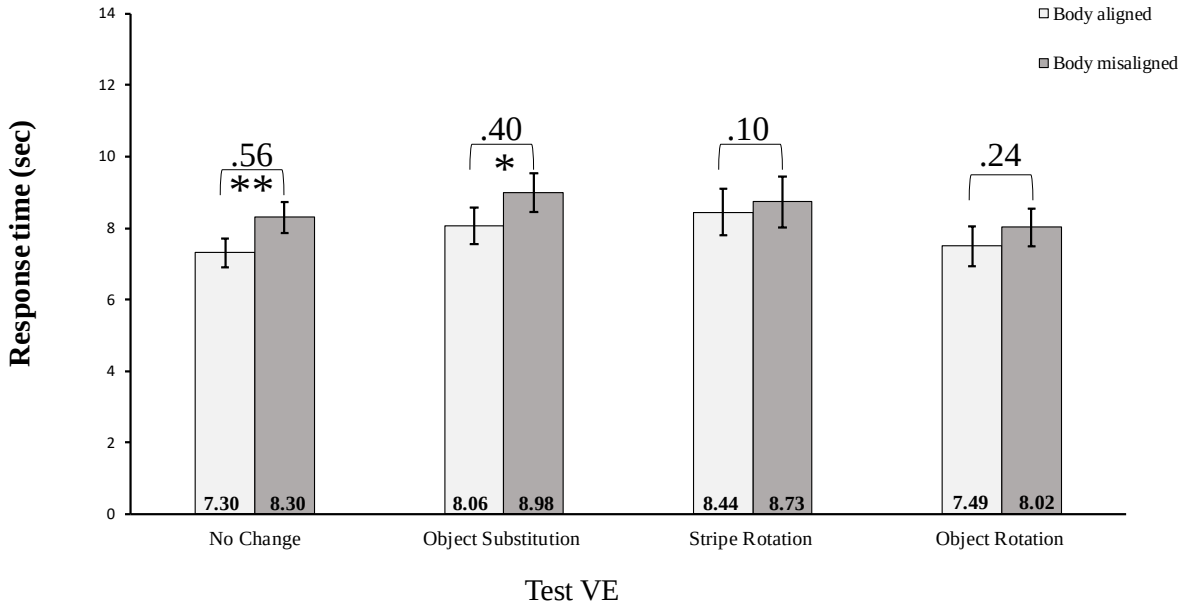


Figure 15. Response latency (sec) for the 90° and 270° imagined perspectives as a function of test environment in Experiment 2. Error bars represent +/- 1 standard error. Effect size (in Hedge's $g_{average}$) is presented above the brackets.
Note. $*p < .05$, $** p < .01$

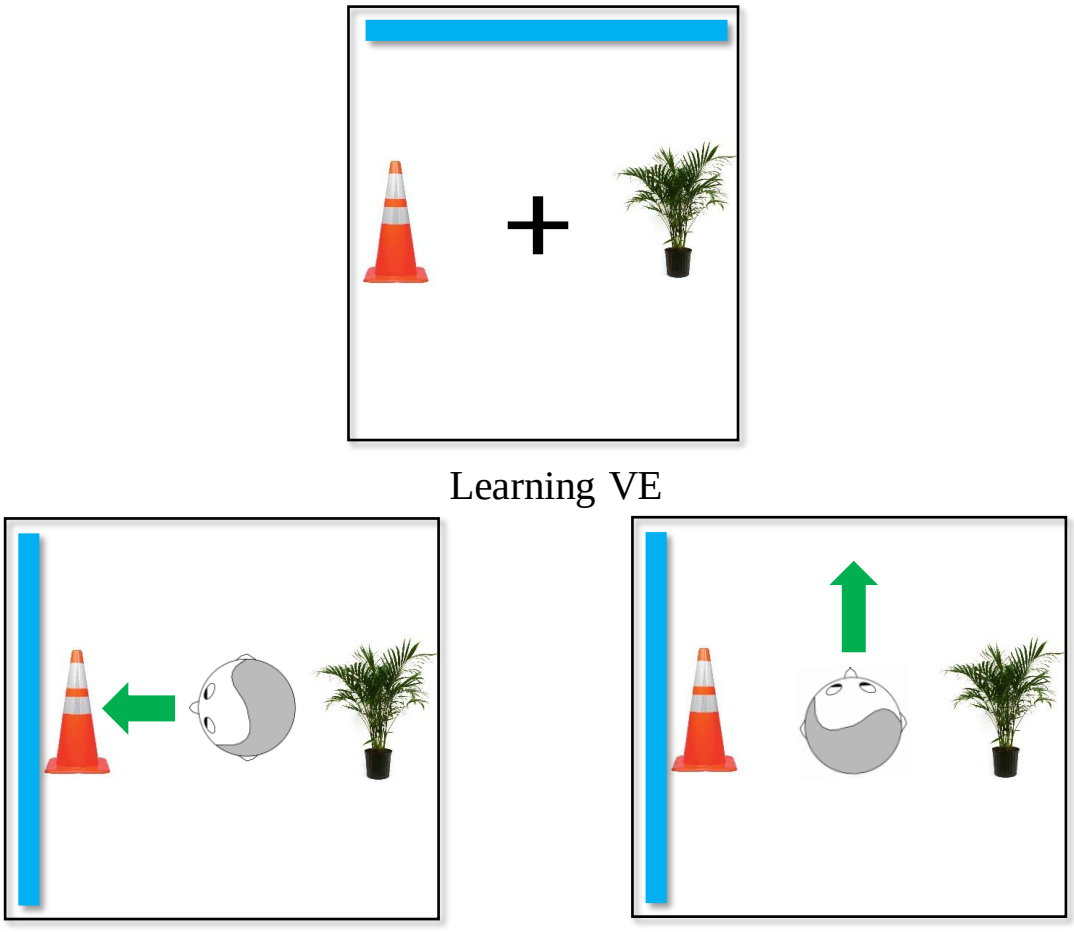


Figure 16. Schematic of the learning and test virtual environments (VEs) for the proposed follow-up study. Clockwise, from top, learning VE, stripe rotation VE with participant facing no cue conflict at test, and stripe rotation VE with participant facing cue conflict at test.

APPENDIX. IRB APROVAL

IOWA STATE UNIVERSITY
OF SCIENCE AND TECHNOLOGY

Institutional Review Board
Office for Responsible Research
Vice President for Research
2420 Lincoln Way, Suite 202
Ames, Iowa 50014
515 294-4566

Date: 1/6/2018

To: Dr. Jonathan W Kelly
W112 Lagomarcino

From: Office for Responsible Research

Title: Human navigation in virtual environments

IRB ID: 09-517

Approval Date:	1/5/2018	**Date for Continuing Review:**	1/7/2020
Submission Type:	Continuing Review / Modification	**Review Type:**	Expedited

The project referenced above has received approval from the Institutional Review Board (IRB) at Iowa State University according to the dates shown above. Please refer to the IRB ID number shown above in all correspondence regarding this study.

To ensure compliance with federal regulations (45 CFR 46 & 21 CFR 56), please be sure to:

- **Use only the approved study materials** in your research, **including the recruitment materials and informed consent documents that have the IRB approval stamp.**
- **Retain signed informed consent documents for 3 years after the close of the study**, when documented consent is required.
- **Obtain IRB approval prior to implementing any changes** to the study by submitting a Modification Form for Non-Exempt Research or Amendment for Personnel Changes form, as necessary.
- **Immediately inform the IRB of (1) all serious and/or unexpected adverse experiences** involving risks to subjects or others; and (2) **any other unanticipated problems involving risks** to subjects or others.
- **Stop all research activity if IRB approval lapses**, unless continuation is necessary to prevent harm to research participants. Research activity can resume once IRB approval is reestablished.
- **Complete a new continuing review form** at least three to four weeks prior to the **date for continuing review** as noted above to provide sufficient time for the IRB to review and approve continuation of the study. We will send a courtesy reminder as this date approaches.

Please be aware that IRB approval means that you have met the requirements of federal regulations and ISU policies governing human subjects research. **Approval from other entities may also be needed.** For example, access to data from private records (e.g. student, medical, or employment records, etc.) that are protected by FERPA, HIPAA, or other confidentiality policies requires permission from the holders of those records. Similarly, for research conducted in institutions other than ISU (e.g., schools, other colleges or universities, medical facilities, companies, etc.), investigators must obtain permission from the institution(s) as required by their policies. **IRB approval in no way implies or guarantees that permission from these other entities will be granted.**

Upon completion of the project, please submit a Project Closure Form to the Office for Responsible Research, 202 Kingland, to officially close the project.

Please don't hesitate to contact us if you have questions or concerns at 515-294-4566 or IRB@iastate.edu.